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Propagation and Use of *Spartina alterniflora* for Shoreline Erosion Abatement

by

W.W. Woodhouse, Jr., E.D. Seneca, and S.W. Broome

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Experimental plantings to stabilize eroding shorelines in Bogue Sound in 1974 were successful. Better stands were produced on sites subject to severe wave stress by reducing transplant spacing to 1.5 to 2 feet apart. Rhizomes without well-developed culms attached were worthless as propagules within the intertidal zone. Seeding was unsuccessful due to exposure to excessive wave energy.

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Differences between plants from different sources decreased with time but a local plant stock was superior to an introduced stock under stressed conditions through the first growing season. Greenhouse-grown plants were more costly but no better than field-grown plants.

Some of the adaptation of *Spartina alterniflora* to the low oxygen supply and the ammonium form of nitrogen characteristic of the intertidal zone were confirmed by laboratory studies. Plants were detrimentally affected by forced aeration of roots and the substitution of nitrate for ammonium. Stands of *Spartina alterniflora* continued to respond to high inputs of nitrogen and phosphorus through the fourth year.

PREFACE

This report is published to assist coastal engineers in shoreline stabilization by the establishment and development of marsh vegetation. The work was carried out under the coastal ecology research program of the U.S. Army Coastal Engineering Research Center (CERC).

The report was prepared by W.W. Woodhouse, Jr., Professor of Soil Science, E.D. Seneca, Associate Professor of Botany and Soil Science, and S.W. Broome, Research Associate in Soil Science, North Carolina State University, Raleigh, North Carolina, under CERC Contract Nos. DACW72-72-C-0015, DACW72-72-C-0012, and DACW72-74-C-0014. Laboratory studies (Section V, Mineral Nutrition) were conducted by R.B. Stryker, Research Associate in Soil Science, R.J. Volk, Professor of Soil Science, P.L. Minotti, visiting Associate Professor of Soil Science, and W.A. Jackson, Professor of Soil Science, North Carolina State University. Support was received from the North Carolina Sea Grant Program, Office of Sea Grant, National Oceanic and Atmospheric Administration, Department of Commerce, Grant Nos. GH-103, 2-35178, and 04-3-158-40; North Carolina Center for Marine and Coastal Studies; and the North Carolina Agricultural Experiment Station.

The authors express appreciation to the personnel of Cape Hatteras and Cape Lookout National Seashores, National Park Service; U.S. Army Engineer District, Wilmington; and North Carolina Highway Commission for their cooperation; and to A.W. Cooper for his advice and encouragement in the initiation of these studies. Special thanks to D.M. Bryan, C.L. Campbell, Jr., and U.O. Highfill for their assistance in all phases of the fieldwork, and to R.P. Savage, Chief, Research Division, CERC, for his advice and encouragement throughout the course of these studies.

Mr. R.M. Yancey, Chief, Ecology Branch, was the CERC contract monitor for the report, under the general supervision of Mr. R.P. Savage, Chief, Research Division.

Comments on this publication are invited.

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JOHN H. COUSINS
Colonel, Corps of Engineers
Commander and Director

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CONVERSION FACTORS, U. S. CUSTOMARY TO METRIC (SI) UNITS OF MEASUREMENT

U.S. customary units of measurement used in this report can be converted to metric (SI) units as follows:

Multiply	by	To obtain
inches	25.4	millimeters
	2.54	centimeters
square inches	6.452	square centimeters
cubic inches	16.39	cubic centimeters
feet	30.48	centimeters
	0.3048	meters
square feet	0.0929	square meters
cubic feet	0.0283	cubic meters
yards	0.9144	meters
square yards	0.836	square meters
cubic yards	0.7646	cubic meters
miles	1.6093	kilometers
square miles	259.0	hectares
acres	0.4047	hectares
foot-pounds	1.3558	newton meters
ounces	28.35	grams
pounds	453.6	grams
	0.4536	kilograms
ton, long	1.0160	metric tons
ton, short	0.9072	metric tons
degrees (angle)	0.1745	radians
Fahrenheit degrees	5/9	Celsius degrees or Kelvins[1]

[1] To obtain Celsius (C) temperature readings from Fahrenheit (F) readings, use formula: $C = (5/9)(F - 32)$. To obtain Kelvin (K) readings, use forumla: $K = (5/9)(F - 32) + 273.15$.

PROPAGATION AND USE OF *SPARTINA ALTERNIFLORA* FOR SHORELINE EROSION ABATEMENT

by

W. W. Woodhouse, Jr.,
E. D. Seneca, and *S. W. Broome*

I. INTRODUCTION

This report contains the results of experiments in the use of marsh vegetation to protect eroding shorelines, a laboratory study on mineral nutrition of *Spartina alterniflora*, and an additional year of monitoring several trials previously described by Woodhouse, Seneca, and Broome (1974). They reported on the role and importance of salt marshes, the biology of *Spartina alterniflora*, and the characteristics of the North Carolina coast. Kadlec and Wentz (1974) also provide additional background information.

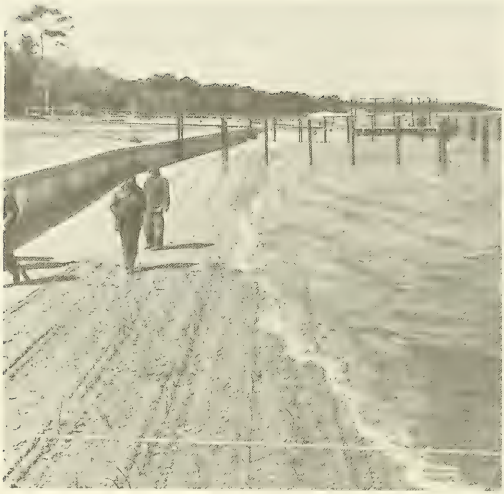
II. PROCEDURE

1. Experimental Sites.

The work started in 1974 was mostly near Pine Knoll Shores and the Pine Knoll Shores Golf Course. Pine Knoll Shores is a residential development along the south shore of Bogue Sound, about 6 miles west of Morehead City, North Carolina. In this vicinity, the shore lies approximately east to west, the fetch is 1.5 miles to the north, 3 miles to the northwest, and 4 miles to the northeast. Tidal range is around 2 to 2.5 feet plus frequent substantial wind setup. Substrate is sandy (99.5-percent sand, 0.2-percent silt, 0.3-percent clay) with some peat patches from old marsh surfaces. The intertidal zone of most of this shoreline was a *Spartina alterniflora* marsh before development. During development a channel was dredged parallel to and about 100 to 150 feet offshore from the present high tide line. The dredged material was deposited along the waterfront lots, covering and killing the marsh. Shoreline recession followed development, and in 1973 a concrete pile bulkhead was installed, just above the existing high tide line (Fig. 1). Erosion continued, causing concern by the owners as to the long-term stability of the bulkhead. This concern prompted the use of the area for experimental planting in 1974.

The Pine Knoll Shores Golf Course is on the sound shore, about 1 mile east of the Pine Knoll Shores experimental site. The shoreline differs from the latter; it has not been bulkheaded and patches of marsh exist with an eroding shoreline between the marsh patches.

These new sites are exposed to northerly winds which create turbulence and affect water levels. Strong northwest winds produce low water while winds from the northeast raise water levels. The plantings on these sites were subjected to rigorous wave action.



9 April 1974

4 April 1975

Figure 1. Views of Pine Knoll Shores.

2. Measurements.

Field experimentation was emphasized with support as needed from the laboratory, phytotron, and greenhouse. Most variables were tested in replicated trials; exploratory and field-scale plantings were not replicated.

The following measures were used to estimate plant growth and development in the field:

(a) Aerial dry weight. Oven dry weight of aboveground growth per transplant (hill) or per unit area.

(b) Belowground dry weight (rhizomes and roots). Oven dry weight of rhizomes and roots of first-year transplants; for older plantings two cores were usually taken from each quadrat harvested for aboveground growth. Samples were taken 30 centimeters deep with a stainless steel coring tube 8.5 centimeters in diameter. Samples were washed and plant parts were separated, weighed, and recorded as belowground growth per hill or per unit area.

(c) Number of flowers. Number of flowering culms per hill or per unit area.

(d) Number of center culms. Number of culms (stems) clustered around the original transplant (recorded for first-year transplants only).

(e) Number of rhizome culms. Number of culms growing from rhizomes away from the original transplant (spread: recorded on first-year transplants only).

(f) Height. Distance from base to tip of culm in centimeters (usually the average of five culms per transplant).

(g) Basal area. Area covered by culms at ground level. This was determined by measuring the cross-sectional diameter of tightly bunched culms; data were recorded per hill or per unit area.

The exposed location and unstable conditions of many shoreline sites make them more vulnerable to damage or total loss than is typical of upland studies; higher experimental errors are usually obtained from coastal studies. Compensation for this problem was attempted through duplication of field tests, wherever possible. Hazards to new plants were: Erosion or sand deposition due to wave action, undermining resulting from channel shifting, and burial by windblown sand.

Growth data were collected near the end of each growing season. Some nondestructive measurements were taken during the first week in

April 1975 on a few of the 1974 experiments to obtain overwinter changes in first-year plantings, and to better evaluate these treatments for shoreline protection.

3. Laboratory Studies.

All plants used in the laboratory experiments were germinated from seed collected in 1972 at Oregon Inlet, North Carolina. The seeds were stored in seawater (2- to 3-percent salt) at 2° to 3° Celsius. Before germination, the seeds were immersed 10 minutes in a 25-percent clorox solution, rinsed thoroughly in distilled water, and placed in a fungicide solution (0.25 gram of Thiram-75 [tetramethylthiuramidisulfide] per 100 milliliters for 5 minutes). The seeds were removed without rinsing and scattered evenly on a tray over paper towels saturated with a 10^{-4} molar solution of calcium sulfate ($CaSO_4$). The tray containing the seed was covered with saran to minimize evaporation and to allow light to reach the seed; small slits in the saran allowed air exchange. The tray was placed in an environment with a diurnal photo period of 14 hours' daylight and 10 hours' darkness until germination (about 1 week). Seedlings were selected from the tray for transfer to a hydroponic culture when they had a 4-centimeter-high green shoot and two roots 5 to 10 millimeters long.

Table 1. Nutrient solutions employed for nitrogen source and aeration experiments with *Spartina alterniflora*.

Treatment	Salt[1]	Concentration
	Basic medium	
Magnesium sulfate	$MgSO_4$	0.25 m$\underline{M}$
Calcium chloride	$CaCl_2$	1.50 m$\underline{M}$
Potassium phosphate	KH_2PO_4	0.25 m$\underline{M}$
Sodium chloride	NaCl	85.30 m$\underline{M}$
Calcium carbonate	$CaCO_3$	0.50 g L^{-1}
Ferric ethylene diamine tetraacetate	FeEDTA[2]	0.90 mg L^{-1}
	Nitrogen variables added to basic medium	
Ammonium chloride	NH_4Cl	4.0 mM
Potassium chloride	KCl	4.0 m$\underline{M}$
Potassium nitrate	KNO_3	4.0 m$\underline{M}$
Ammonium chloride	NH_4Cl	2.0 m$\underline{M}$
Potassium nitrate	KNO_3	2.0 m$\underline{M}$
Potassium chloride	KCl	2.0 m$\underline{M}$

1. Micronutrients added at one-half the concentration given by Hoagland and Arnon (1950).

2. Added every 5 days.

Except where indicated, all plants used in this study were grown in the solutions listed in Table 1. Calcium carbonate was used to buffer the solutions at hydrogen-ion concentration (pH) 7.1 to 7.4.

In the first two experiments, plants were supported by placement in a 4-centimeter-thick layer of polypropylene black beads, 2 millimeters in diameter and a density of 0.9 gram per cubic centimeter, which floated on the surface of the nutrient solution. Although the beads worked well for plant support, algae growth and difficulty in changing nutrient solution limited their use. Thus, in the last three experiments, plants were supported in plastic cups mounted in a removable lid which allowed solution renewal and prevented algae growth.

III. PROPAGATION

Spartina alterniflora propagates vegetatively and by seeds. New sites are usually colonized by seeds that germinate in March in North Carolina. Fragments of marsh sod may become dislodged by water or ice, drift onto bare sites, take root, and spread. New stands thicken and spread through the growth of new plants from rhizome culms and seedlings. Seedlings and vegetative transplants usually produce seed the year of establishment; the amount depends on the growth and vigor of the stand.

This section provides data from several tests on eroding shorelines plus 1 year's observations of two previously reported experiments (Woodhouse, Seneca, and Broome, 1974).

1. Pruning.

In machine planting it is sometimes convenient to prune large transplants to facilitate handling. However, earlier observations suggest that pruning may be detrimental to survival and early regrowth. The effect of pruning and the relative importance to the reestablishment process of the leaves versus stems and buds versus rhizomes alone are presented in Table 2. The plots extending from above mean high water (MHW) to below mean low water (MLW) were planted near the optimum date for this species in the area. The intertidal nursery area at Beaufort, North Carolina, was the source for the plants and rhizomes.

Variability in this experiment was high, due largely to erosion. There was no significant difference in the growth of pruned and unpruned plants. The rhizome planting yielded clearcut results; rhizomes without attached plants succumbed. The results of these treatments may be compared in Figures 2, 3, and 4.

These findings are worthy of some emphasis since the use of *Spartina alterniflora* rhizomes for transplanting continues to be suggested. This plant spreads into bare areas by rhizomes, with new plants growing from new rhizomes; these young plants make excellent transplants. However,

Table 2. Effect of pruning on growth of transplants planted 17 April 1974 at Pine Knoll Shores (plot size 9 by 50 feet, three replications).

Treatment	Sampled 14 October 1974[1] Aerial dry wt. (g/plant)	Flowers/ plant	Center culms/ plant	Rhizome culms/ plant	Height (centimeter)	Basal area (centimeter²/ meter²)	Percent survival	4 April 1975 Culms/ meter²	Height (centimeter)
Check plot	52.6	5.2	18.5	15.7	113	17.7	28.7	82	21
Leaves removed[2]	39.6	1.0	8.2	8.7	108	13.9	34.7	73	27
Tops removed[3]	37.5	2.3	11.0	12.2	98	11.4	25.7	24	16
Rhizome culms[4]	30.5	1.3	8.5	12.0	78	8.9	32.0	50	17
Rhizomes[5]	0.0	0.0	0.0	0.0	0	0.0	0.0	0	0
LSD Treatment									
0.01	--[6]	--[6]	--[6]	--[6]	--[6]	--[6]	--[6]	--[6]	--[6]
0.05	--[6]	--[6]	--[6]	--[6]	22	--[6]	--[6]		
CV%	101.4	119.5	90.7	90.9	17.9	51.3	42.4		

1. Plant spacing 2 by 3 feet or 0.56 square meter per plant.

2. All unrolled leaves removed.

3. Bud and rolled leaves removed.

4. Young plants, 12 centimeters or more in length attached to rhizomes.

5. Healthy rhizomes without emergent culms; this treatment omitted from statistical analysis.

6. Not significant.

Figure 2. Unpruned transplants planted 17 April 1974 (photo taken 4 April 1975).

Figure 3. Culms with rhizomes attached planted 17 April 1974 (photo taken 4 April 1975).

Figure 4. Rhizomes without culms planted 17 April 1974 (photo taken 4 April 1975).

leaving these plants attached to the parent rhizomes improves neither survival nor early regrowth.

The absence of emerging plants from the rhizome propagules is not surprising since the roots and rhizomes of this plant are dependent upon the leaves and connecting shoots for oxygen supply (Teal and Kanwisher, 1966; Anderson, 1974). Until contrary evidence is found, the planting of rhizomes without culms in the intertidal zone is discouraged. Rhizomes without culms are difficult to harvest and transplant, and are useless as disseminules.

2. Pretransplanting Treatment.

Although established plants in sandy substrates in North Carolina frequently respond to fertilizer, the benefits from fertilizing at transplanting have been difficult to demonstrate. This is due to the absence in transplants of a developed root system capable of absorbing a significant quantity of applied nutrients. An experiment in providing stimulation to transplants by fertilizing a few weeks before digging, while roots are intact, is presented in Table 3. Although there was some indication of benefit from these applications, the results were inconsistent. This was probably because the erosion induced high variability.

3. Fertilization at Transplanting.

On an eroding shoreline early growth stimulation of transplants could improve survival. The experiment outlined in Table 4 tested the feasibility of hastening the growth of transplants by fertilization at planting. Although some benefit appeared from these treatments about 60 days after transplanting, by the end of the growing season the evidence had disappeared. If there was some initial response to applied nutrients, it did not materially affect the final establishment of vegetation.

4. Greenhouse Versus Field-Grown Transplants.

Spartina alterniflora plants grown from seed in peat pots were compared with field-grown plants by transplanting both at Pine Knoll Shores (Table 5). The experiment was planted about 1 month later than most of the Pine Knoll Shores experiments. Growth and spread were slow in comparison with other plantings in the area. Although results were variable and inconclusive, it is concluded that peat-pot plants can be justified only where these plants are markedly superior, or where suitable field-grown plants are unavailable. The latter will apply in many situations unless at least 1 year of planning and preparation precedes planting.

Table 3. Nitrogen and phosphorus effects on growth of plants removed from the nursery area at Beaufort and transplanted at Pine Knoll Shores.[1]

N Rate (kg/ha)	Aerial Dry Weight (g/plant)		Flowers/Plant		Center Culms/Plant		Percent Survival	
	P Rate (kg/ha)							
	0	25	0	25	0	25	0	25
0	115.6	64.8	10.4	5.4	25.2	18.7	43.6	28.9
112	73.5	109.5	5.2	8.0	14.3	17.7	31.1	52.0
LSD:[2]								
N x P								
0.01	41.0		3.5		--[3]		13.7	
0.05	30.3		2.6		--[3]		10.1	
CV%[4]	34.3		36.1		46.4		26.8	

N Rate (kg/ha)	Rhizome Culms/Plant		Height (cm)		Basal Area (cm^2/m^2)	
	0	25	0	25	0	25
0	32.6	20.7	127	121	46.3	24.7
112	23.2	28.2	125	140	28.0	37.7
LSD:[2]						
N x P						
0.01	--[3]		--[3]		16.2	
0.05	--[3]		--[3]		12.0	
CV%[4]	54.3		13.6		36.0	

1. Nursery fertilized 5 March 1974; transplanted 9 April 1974; harvested 11 October 1974.

2. Least significant difference. (There were no significant main effects due to nitrogen or to phosphorus.)

3. Not significant.

4. Coefficient of variation.

Table 4. Effect of furrow application of nitrogen and phosphorus at transplanting.[1]

Sampled 11 October 1974 — P Rate (kg/ha)

N Rate (kg/ha)	Rhizome Culms/Plant		Height		Basal Area (cm^2/m^2)		Percent Survival	
	0	25	0	25	0	25	0	25
0	9.4	15.4	113	109	14.0	15.4	85.6	83.6
112	17.8	19.7	132	116	23.4	18.5	60.1	68.6
LSD:[2]								
N 0.01	--[5]		--[5]		--[5]		12.1[4]	
0.05	--[5]		10.5		6.2		8.9	
CV%[3]	78.5		13.0		50.9		17.4	

Sampled 11 October 1974 — P Rate (kg/ha)

N Rate (kg/ha)	Aerial Dry Weight (g/plant)		Flowers/Plant		Center Culms/ Plant	
	0	25	0	25	0	25
0	36.4	41.6	4.9	6.7	12.9	11.6
112	47.6	57.6	7.1	9.3	15.4	15.6
LSD:[2]	No Significant Difference					
CV%[3]	48.0		56.4		44.7	

Sampled 3 April 1975 — P Rate (kg/ha)

N Rate (kg/ha)	Culms/m^2		Height (cm)	
	0	25	0	25
0	95	118	32	36
112	97	83	32	35

1. Transplanted 17 April 1974.

2. Least significant difference.

3. Coefficient of variation.

4. No significant N x P interactions, nor any significant phosphorus effect.

5. Not significant.

Table 5. Comparison of greenhouse-grown and field-grown transplants at Pine Knoll Shores.[1]

Origin of Seed	Method of Production	Treatment	Aerial Dry Weight/ Plant	Flowers/ Plant	Center Culms/ Plant	Rhizome Culms/ Plant	Height (cm)	Basal Area (cm^2/m^2)
Oregon Inlet	Greenhouse	Saltwater	5.2	1.0	6.3	4.1	55.6	1.5
Beaufort	Greenhouse	Saltwater	13.0	1.6	9.8	7.3	58.2	4.9
Oregon Inlet	Greenhouse	Freshwater	9.1	2.0	9.3	7.2	68.2	3.9
Beaufort	Greenhouse	Freshwater	7.5	0.4	6.2	8.3	52.6	2.1
Beaufort	Field	--	24.6	2.2	12.3	3.6	95.3	7.3
Oregon Inlet	Field	--	13.0	2.0	6.6	2.6	92.2	3.5
LSD[4] Treatment	0.01		--[5]	--[5]	--[5]	--[5]	21.7	--[5]
	0.05		11.4	--[5]	--[5]	--[5]	16.2	--[5]
CV%[6]			99.0	98.6	66.6	104.2	24.1	151.2

1. Transplanted 15 May, Sampled 14 October 1974, plot size 9 by 25 feet, three replications spaced 2 by 3 feet.

2. Subjected to saltwater prior to transplanting.

3. Transplanted without salt treatment.

4. Least significant difference.

5. Not significant.

6. Coefficient of variation.

5. Sources of Variability at Pine Knoll Shores.

First inspection of the Pine Knoll Shores site suggested uniform substrate, but the variable growth of the plantings indicated sharp variations in substrate. Corings in April 1975 revealed no apparent basis for this assumption. The substrate-related differences in growth of *Spartina alterniflora* were confined to a few patches of peaty remains of old marsh surfaces as shown in Figure 5. Transplanting on these was difficult and both survival and growth were poor.

The construction of elevated walks and docks in front of many of the residences contributed to the high variability but was not the major cause (Fig. 6).

The high variability in growth and in spread within these plantings was probably caused by movement of the substrate surface. Minor changes in the surface affect growth which, in turn affects loss and accumulation of sediments. Cause and effect become so intertwined that a clear separation is impossible. Where growth is above average there is evidence of either accretion or sediment retention (Fig. 7). This makes comparison of small-scale plantings intermingled with unsuccessful plantings difficult.

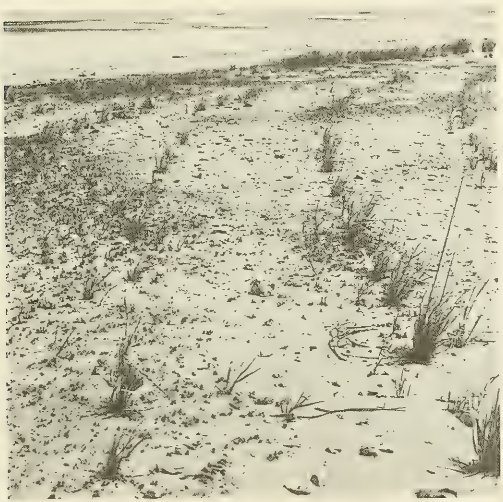
The presence of the bulkhead close to the normal high tide line aggravated this problem. Most of the plantings next to the bulkhead were destroyed by wave action before winter (Fig. 8). Erosion was reduced where plants had survived and grown.

6. Source of Plants.

Previous work has shown definite differences in transplants taken from different locations. Fourth-year data from an experiment at Snow's Cut, North Carolina, are presented in Table 6. Differences between sources are diminishing with time. Factors other than source, i.e., elevation and competition from invading species, become important as plantings mature. Also, how much one source has spread into another is unsure. The results from this experiment confirm that transplants from each of the five locations would be satisfactory on this site.

A comparison of the results from an experiment at Pine Knoll Shores involving transplants grown in an intertidal nursery at Beaufort from two seed sources is shown in Table 7. Pine Knoll Shores has an eroding shoreline, a more stressed situation than that at Snow's Cut. This condition has magnified the difference between the local (Beaufort) source (Fig. 9) and the foreign (Oregon Inlet) source (Fig. 10). At the end of the first growing season, the Beaufort plants were distinctly superior. Although both sources survived the winter, erosion was more severe on the thinner, shorter stands of the Oregon Inlet plants.

17 May 1974



4 April 1975

Figure 5. Old marsh surface, Bogue Sound, North Carolina.

Figure 6. Construction in front of Pine Knoll Shores, 22 May 1974.

Figure 7. Humps in soil surface behind thick grass growth, 4 April 1975.

Figure 8. Vegetative groins planted 18 April 1974. Note eroded upper beach (photo taken 4 April 1975).

Table 6. Effect of transplant source and elevation on the development of *Spartina alterniflora* in the fourth growing season at Snow's Cut.

Transplant Source	Culms/ m^2	Flowers/ m^2	Height (cm)	Aboveground yield (kg/ha)
	Average across four elevation zones			
Oregon Inlet	208	78	135	7,690
Ocracoke	172	59	144	8,960
Beaufort tall	180	22	116	5,010
Beaufort short	140	35	138	6,840
Snow's Cut	155	27	135	6,420

Elevation (Average period inundated hr/ day)	Culms/ m^2	Flowers/ m^2	Height (cm)	Aboveground yield (kg/ha)
	Mean of Five Sources			
0.0 to 3.5	122	19	106	2,790
3.6 to 8.8	152	36	121	4,950
8.9 to 12.9	176	43	145	7,910
13.0 to 16.6	234	86	163	12,280

Table 7. Comparison of plants from Beaufort and Oregon Inlet seed grown at Beaufort. Transplanted 18 April 1974 at Pine Knoll Shores.

Source of planting stock		Sampled 14 October 1974[1]					
		Aerial dry weight (g/plant)	Flowers/ plant	Center culms/ plant	Rhizomes culms/ plant	Height (cm)	Basal area (cm^2/m^2)
Beaufort		101.3	6.0	29.0	19.1	132	28.8
Oregon Inlet		26.8	4.6	12.6	15.1	95	8.3
LSD[2]							
Treatment	0.01	28.8	-[3]	12.2	-[3]	35	6.5
	0.05	20.5	-[3]	8.7	-[3]	25	4.7
CV%[4]		31.2	69.0	40.9	70.6	21.2	24.4

	Sampled 4 April 1975	
	Culms/ m^2	Height (cm)
Beaufort	201	33
Oregon Inlet	87	20

1. Spacing 2 by 3 feet or 0.56 square meter per plant.

2. Least significant difference.

3. Not significant.

4. Coefficient of variation.

Figure 9. Beaufort plants planted 18 April 1974 in rows 3 feet apart. Garden label in center is on outside row; label on left indicated width of spread (photo taken 3 April 1975).

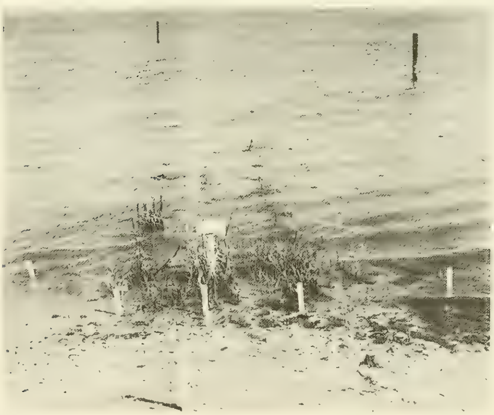


Figure 10. Oregon Inlet plants. Three center labels on the three rows; outer labels at edge of spread.

In spite of the distinct first-year disadvantage suffered by the Oregon Inlet plants, the April 1975 culm counts suggest that these plants are increasing.

In summary, the local source has a distinct advantage during the establishment period and would succeed where an introduced grass could fail. The April 1975 data suggest that, if it survives the first winter, the foreign source may improve with time and prove adequate for the new location.

7. Date and Elevation of Seeding.

Seedings were made in April 1972 at Beaufort on dredge spoil. A 21 June seeding in the low elevation zone was added after part of the April seeding was destroyed by a late May storm. An exploratory seeding in the high elevation zone was made 21 June to find a way of quickly stabilizing this zone. Late seeding reduced the first-year growth (Woodhouse, Seneca, and Broome, 1974) but this difference disappeared by the third year (Table 8). Although seeding was successful in the high zone, above its usual elevation, it will probably be replaced by other species. However, this is a practical and economical way to stabilize this zone.

8. Seeding Experiments at Pine Knoll Shores.

Three seeding experiments were initiated at this site in April 1974 and several seeding treatments were included in transplanting experiments. Several days of strong northerly winds in early May, after germination occurred, completely destroyed all the seeding tests along the shore. Seeding is not a reliable approach under these conditions but could succeed if the northerly winds came at a less critical time.

IV. SHORELINE PROTECTION

Shoreline stabilization and erosion abatement will often be a major objective of marsh restoration or establishment. The findings from the following three plantings relate to some aspect of shoreline stabilization.

1. Sediment Trapping.

The plantings at Snow's Cut were made during April 1971 and their development to November 1973 was presented in Woodhouse, Seneca, and Broome (1974). Shortly after planting, survey lines were established through three planted blocks and through four unplanted areas between the blocks (Fig. 11). Changes in elevation were assumed to be a measure of stabilization. Results from a 13 November 1974 survey are presented in Figures 12 through 18. Except for transect 7 on the downstream side of the experimental area, little net change occurred in the

Table 8. Effect of elevation and seeding date on aerial dry weight the third growing season after seeding. (Sampled 9 October 1974).

Treatment No.	Seeding Date 1972	Elevation Zone (MSL)	Dry Weight (kg/ha)[1] Shoots
1[2]	21 June	4.0 to 4.2	1,663
2	21 June	3.4 to 4.0	3,848
3	11 April	3.4 to 4.0	4,097
4	11 April	3.1 to 3.4	4,395
5	21 June	3.1 to 3.4	3,583
LSD[3]			
Treatment 0.01			1,468
0.05			1,032
CV%[4]			16.1

1. Average of three 2- by 10-foot samples.

2. Other plants in the high elevation zone were 22 kilogram/hectare *Salicornia* species and 16 kilogram/hectare *Fimbristylis* species.

3. Least significant difference.

4. Coefficient of variation.

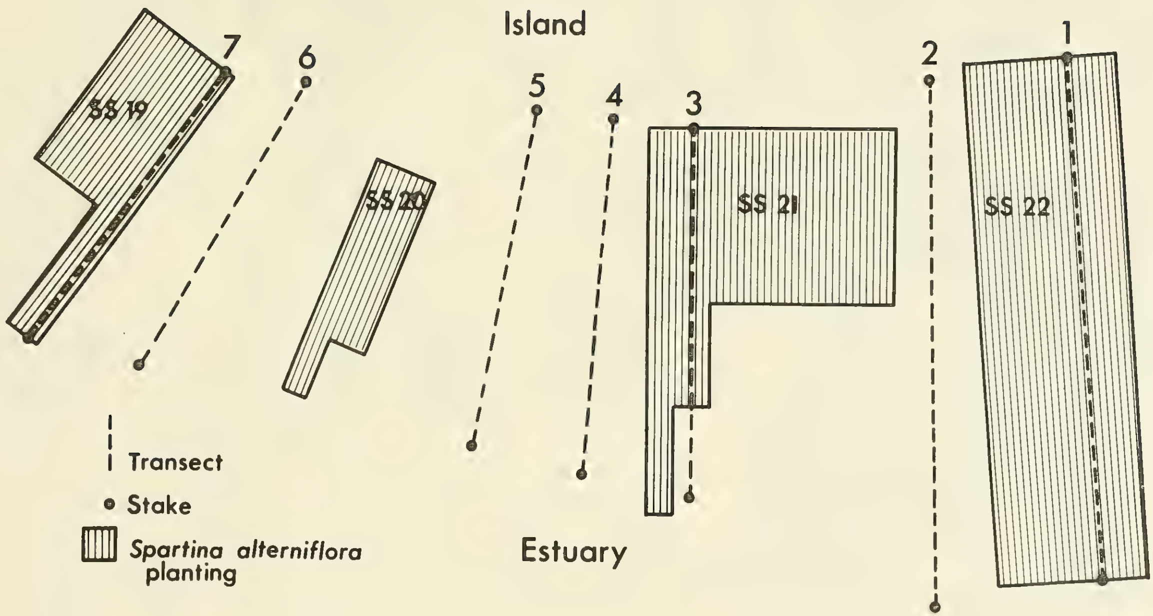


Figure 11. Diagram showing location of transects at Snow's Cut.

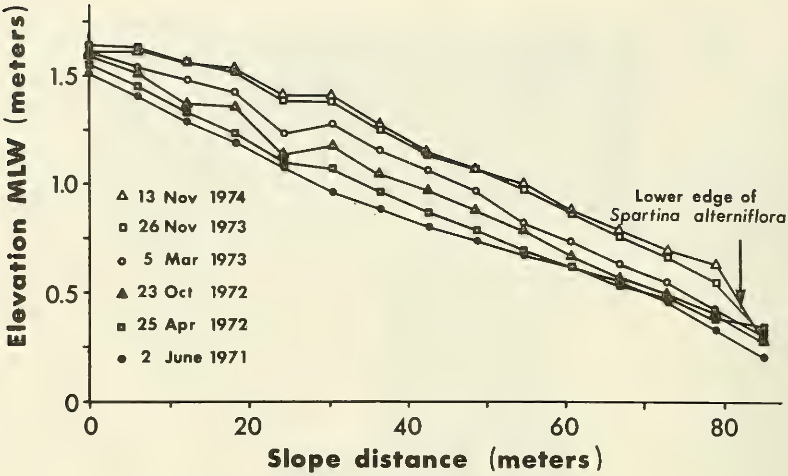


Figure 12. Planted transect No. 1, Snow's Cut; 2 June 1971 to 13 November 1974.

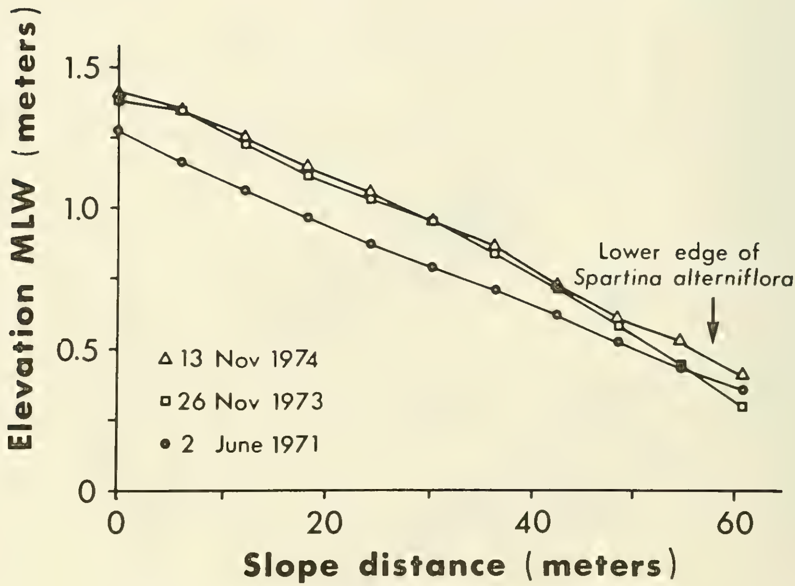


Figure 13. Planted transect No. 3, Snow's Cut; 2 June 1971 to 13 November 1974.

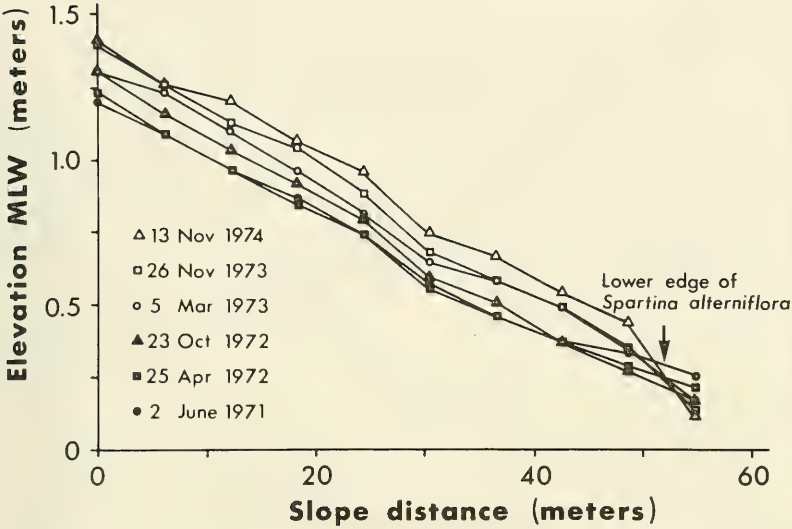


Figure 14. Planted transect No. 7, Snow's Cut; 2 June 1971 to 13 November 1974.

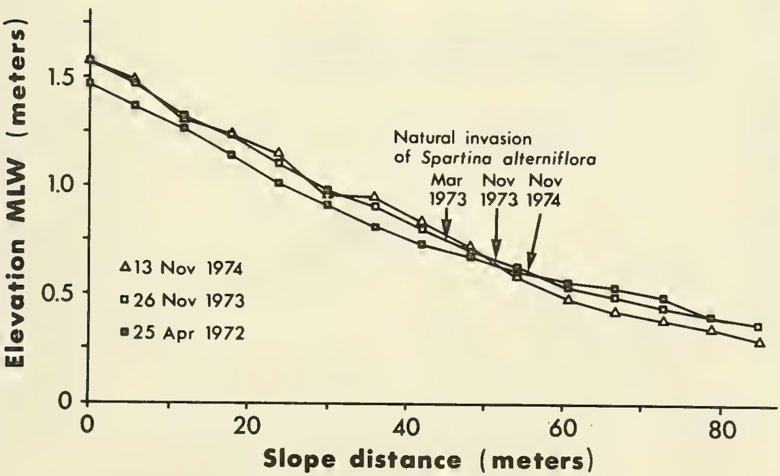


Figure 15. Unplanted transect No. 2, Snow's Cut; 25 April 1972 to 13 November 1974.

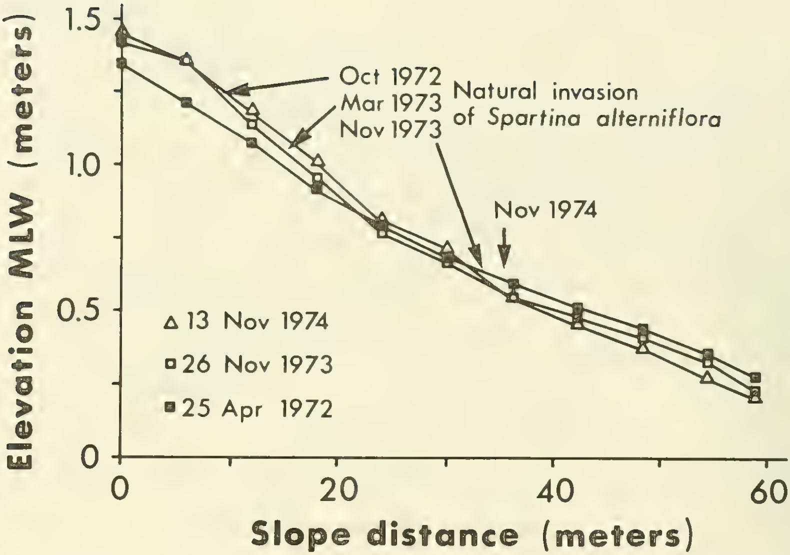


Figure 16. Unplanted transect No. 4, Snow's Cut; 25 April 1972 to 13 November 1974.

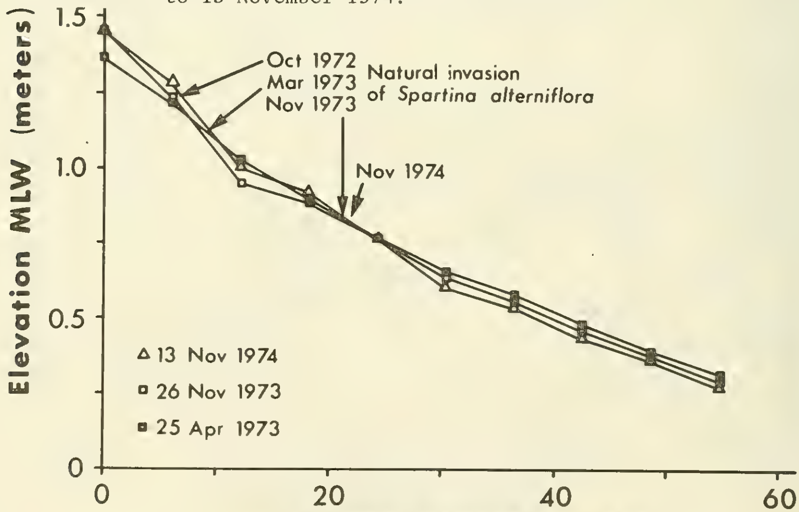


Figure 17. Unplanted transect No. 5, Snow's Cut; 25 April 1972 to 13 November 1974.

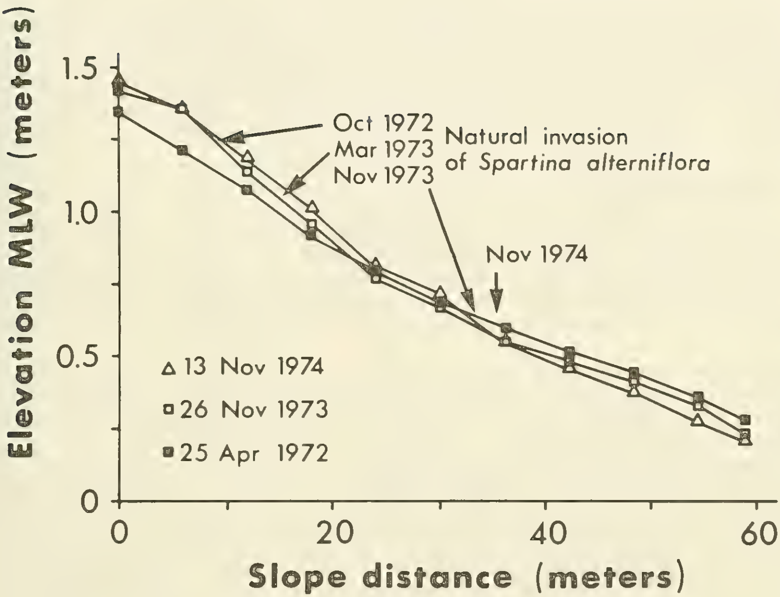


Figure 18. Unplanted transect No. 6, Snow's Cut; 25 April 1972 to 13 November 1974.

planted blocks between November 1973 and November 1974. There was evidence of some accumulation along the unplanted profiles mostly in the middle and upper zones where *Spartina alterniflora* is naturally invading.

Except for transect 7, sediment accumulation by the planted marsh during the 12-month period, November 1973 to November 1974, slowed substantially for no obvious reason. The explanation probably lies in changes in availability and movement of sediments during this period. However, the plantings appear to have stabilized these areas; there was gain on one planted transect and no loss on the others.

2. Plant Spacing.

Spacing of *Spartina alterniflora* transplants is not critical on protected sites. With a reasonable survival rate, areas transplanted 3 by 3 feet in the spring will have complete cover by the next spring. A wider spacing seems questionable since it places more stress on survival rate and does not result in substantial savings.

Under a more rigorous eroding shoreline condition, where the main objective is early stabilization, a close spacing may be justified. A situation was encountered at Pine Knoll Shores where closer spacing appeared to make worthwhile differences. Data taken in the fall showed growth proportional to planting density and nondestructive sampling in the spring indicated little change over winter (Table 9). However, these data do not fully reflect the condition of the surviving plants. This is better seen in Figures 19 and 20. The plants on the 3- by 3-foot spacing were more severely stressed during the winter. Apparently, the closer spacings dampened wave action and reduced sediment movement sufficiently to significantly affect the vigor of the plants. The plants protected one another, and the required critical mass developed between the 2- and 3-foot spacing. Differences between the 2-foot and 1.5-foot spacing were not evident at the end of winter.

The closer spacing did, in this case, improve stand survival and condition and result in more rapid stabilization. The wider spacing may still colonize and cover over later in the year.

3. Pine Knoll Shores Golf Course.

Two actively eroding sections in a natural marsh along the sound shore beside the Pine Knoll Shores Golf Course were used in an experimental planting (Table 10). These gaps originated from excessive filling during and following construction of the golf course. Both gaps were crescent-shaped bays bounded by *Spartina alterniflora* marsh. The gaps probably represented intertidal shoreline indentations that were filled to straighten the shoreline and provide space for the course.

Table 9. Effect of spacing on growth of *Spartina alterniflora*[1] at Pine Knoll Shores.

	Sampled							
	10 October 1974[2]						3 April 1975	
Spacing (ft)	Aerial Dry Wt. (g/m^2)	Flowers/ m^2	Center Culms/ m^2	Rhizome Culms m^2	Height	Basal Area (cm^2/m^2)	Culms/ m^2	Height (cm)
1.5 by 1.5	127.3	11.4	40.2	21.8	132	22.2	125	36
2 by 2	76.2	6.4	27.4	10.8	120	12.5	86	37
3 by 3	39.9	3.6	12.0	13.5	120	7.3	61	24

1. Transplanted 11 April 1974, plot size 40 by 50 feet, three replications.

2. Mean of 20, 1-square-meter samples per treatment.

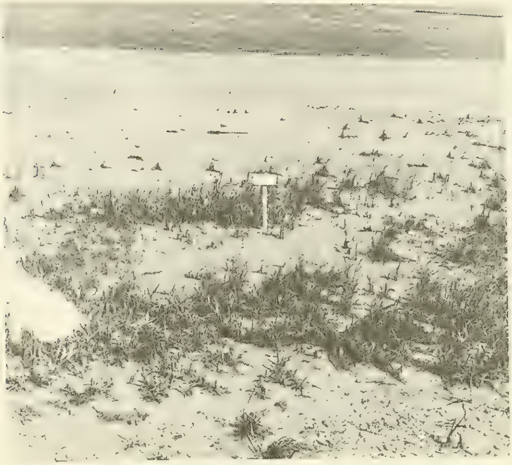


Figure 19. *Spartina alterniflora* spaced 3 by 3 feet, planted 11 April 1974 (photo taken 4 April 1975).

Figure 20. *Spartina alterniflora* spaced 2 by 2 feet, planted 11 April 1974 (photo taken 4 April 1975).

Table 10. Development of *Spartina alterniflora* transplanted 19 May 1974 along an eroding shoreline at Pine Knoll Shores Golf Course.

	Site							
	Bay 1				Bay 2			
	Upper Zone		Lower Zone		Upper Zone		Lower Zone	
	15 Oct 74	3 Apr 75	15 Oct 74	3 Apr 75	15 Oct 74	3 Apr 75	15 Oct 74	3 Apr 75
Flowers/m^2	8	--	4	--	21	--	3	--
Height (cm)	125	55	114	33	158	70	101	37
Basal Area (cm^2/m^2)	34	--	4	--	78	--	5	--
Center Culms/m^2	23	--	25	--	111	--	22	--
Rhizome Culms/m^2	48	--	3	--	51	--	4	--
Culms/m^2	--	304	--	51	--	377	--	60
Dry Weight								
Tops (g/m^2)	126.1	--	29.7	--	337.6	--	25.9	--
Roots (g/m^2)	162.1	--	88	--	465.2	--	176.2	--

Active erosion along the middle part of these crescents was observed before planting. Waves had undercut the turf, leaving a vertical scarp. A few loads of sand dumped along the eroding face provided a plantable upper slope. The two bays were machine-planted about 2 weeks later (Figs. 21 and 22).

The plantings in both bays were unusually successful. Survival was excellent and growth was substantially above average (Fig. 23). The superior growth was apparently due to nutrient supply coming from the adjacent golf fairway and green. The best growth and greenest plants were in the rows nearest the turf; vigor decreased with increasing distance from the turf. Growth on bay 2, which was adjacent to a green, was substantially better than that on bay 1, which bordered the less heavily fertilized fairway. The soil is sandy under both the green and the fairway which lie 1 or more feet higher than the plantings. The movement of nutrients, particularly nitrogen, into the plantings is inevitable. An ample nutrient supply seemed important to the rapid establishment of these plantings.

The primary objective of this planting was to test the feasibility of reestablishing marsh along shoreline that was eroding too rapidly for the natural occurrence of revegetation. The appearance of the plants in early April 1975 (Figs. 24 and 25), supported by culm density counts (Table 10), showed that these plantings were highly successful. Marsh restoration was feasible and the resumption of erosion in these bays is unlikely.

V. MINERAL NUTRITION

1. Laboratory Studies.

The roots of *Spartina alterniflora* normally grow under waterlogged conditions. The plants' ability to produce substantial quantities of dry matter under these conditions implies that the roots can function effectively under low ambient oxygen concentration and when ammonium is the dominant inorganic nitrogen form available. The following experiments were undertaken to determine whether these conditions are optimal for growth. The results indicate that they are. Aeration of the root system and exposure to nitrate nitrogen were both detrimental.

a. Experiment 1. After germination, plants were transferred to a nutrient solution culture of either an ammonium (NH_4), a nitrate, or an ammonium plus nitrate nitrogen supply (Table 1). For each nitrogen source, 20 plants were placed in each of two 4-liter containers, half of which were aerated. All solutions were stirred with a magnetic stirring bar in the bottom of the pot. Nitrogen concentrations were monitored weekly and adjusted to maintain the levels given in Table 1. The plants were grown in a growth chamber at a 16-hour day length and a 29.4° Celsius temperature, and maintained with 1,500-foot candles at the surface of the containers followed by an 8-hour dark period and a temperature of 23.9° Celsius.

Figure 21. Views of bays at Pine Knoll Shores before planting, 17 May 1974.

Figure 22. Planting at Pine Knoll Shores Golf Course, 23 May 1974.

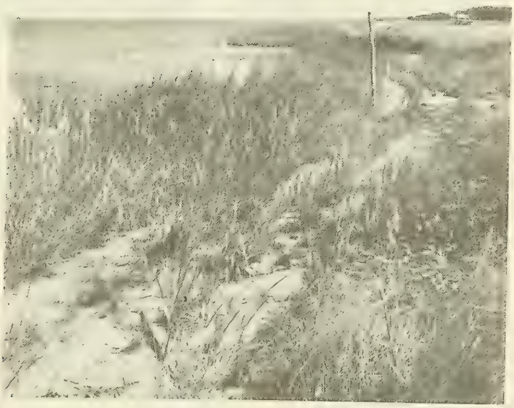


Figure 23. Same scene as Figure 22, 5 months later.

Figure 24. Upper slope at Pine Knoll Shores Golf Course, 4 April 1975.

Figure 25. Lower slope at Pine Knoll Shores Golf Course, 4 April 1975.

After a 6-week growth, the plants were removed, rinsed in distilled water, blotted, and fresh weights determined. Analyses for nitrate reductase (NR), glutamic dehydrogenase (GDH), endogenous NH_4, NO_3, nitrite (NO_2), and buffer-soluble protein were determined on fresh root and shoot tissue.

Fresh weights of roots and shoots (Table 11) indicated that more growth occurred when ammonium was the nitrogen source. Periodic analysis of nutrient solutions indicated that some ammonium was produced in the nonaerated nitrate cultures. This may have been beneficial because ammonium ions were the preferred nitrogen source for uptake. In associated studies when nutrient solutions were changed weekly to minimize ammonification in solution, less fresh weight was produced with nitrate-cultured plants.

Table 11. Fresh weight of shoots and roots after a 6-week growth in nitrogen and aeration treatments.

		Grams fresh wt/plant		
Treatment	Aeration	Shoots	Roots	Total
Ammonium	No	3.50	0.84	4.35
	Yes	3.20	1.10	4.30
Nitrate	No	2.60	0.90	3.50
	Yes	1.20	0.55	1.75
Ammonium plus Nitrate	No	3.40	0.92	4.32
	Yes	2.30	0.90	3.20

Appearance of the nitrate plants indicated more severe growth abnormalities than was evident from the weight data in Table 11. Newly germinated plants placed in nitrate culture developed yellowish leaves and growth rates were restricted for the first 3 to 4 weeks. In the early stages of growth, roots of these plants were spindly and elongated, resembling symptoms of nitrogen-deficient root growth. After 4 to 6 weeks approximately 40 percent of the plants grown in nitrate cultures appeared to overcome these symptoms and began to develop greener leaves and higher growth rates.

At the 4- to 6-week growth stage, rhizome development and tillering are very active processes in the natural growth of *Spartina alterniflora*. Some plants tended to respond more favorably to nitrate nutrition at this stage of growth. However, it should be noted that with nitrate cultures, 60 percent of the plants had difficulty recovering and continued to show symptoms prevalent in earlier growth. One problem encountered throughout this study was high inherent variability in individual plant growth rates, presumably because of genetic factors associated with a wild species. Variability was usually more pronounced in nitrate-cultured plants.

Aeration of nutrient solutions adversely affected growth. With both ammonium and nitrate culture, aeration caused yellowing of the leaves and reduced growth rates. Although fresh weights of ammonium-cultured plants (Table 11) did not reflect adverse effects of aeration, the leaves were yellowish and noticeably affected. The nitrate-cultured plants were severely affected by aeration. To obtain normal plants 6 weeks old or more for further experiments, all nutrient solutions had to be nonaerated. Whether the effects of aeration were directly related to oxygen toxicity or indirectly related to problems such as carbon dioxide accumulation or nutrient availability has not been determined.

Plants grown in nitrate cultures contained nitrate reductase (NR) indicating the capability to reduce nitrate (Table 12). Roots of the nitrate plants contained a much higher NR activity than the shoots did, although these shoots contained higher activity than the shoots from ammonium-cultured plants. Aeration restricted NR in both tissues. The presence of ammonium and nitrate in the external solution dramatically decreased NR in root tissue and decreased a lesser extent in shoot tissue. Nitrate accumulation in roots and shoots was decreased by the presence of ammonium under both aerated and nonaerated conditions. Relatively little nitrate accumulated in shoots which, together with the low NR of the shoots, suggested that little nitrate was translocated from root tissue. Whether the decrease in NR of the root tissue resulting from presence of ammonium was due to an inhibition in the uptake of the inducer (nitrate) or was due to a specific effect of ammonium (or a product of ammonium assimilation) on net enzyme synthesis is unknown. There was little treatment effect on the ammonium or nitrate concentrations in the tissue (Table 12).

Glutamic dehydrogenase (GDH) catalyzes the formation of glutamate from ammonium and α-ketoglutarate. This reaction is the primary process for ammonium assimilation. Activity of GDH was highest in the root system, suggesting that most ammonium assimilation took place in the roots (Table 12). The presence of nitrate and ammonium decreased the GDH activity of roots and shoots under nonaerated conditions. With aeration, the effect was noted only in the roots. Soluble protein content was highest in tissue grown with ammonium. In general, the data indicate that poor growth with nitrate as the nitrogen source was associated with an inability to utilize nitrate effectively.

Table 12. Characteristics of 6-week-old *Spartina alterniflora* as affected by nitrogen source and aeration.

Treatment	Nitrate reductase (μmoles g^{-1} hr^{-1})[1]	Glutamic dehydrogenase (μmoles g^{-1} hr^{-1})	Endogenous NH_4 (μmoles g^{-1})	Endogenous NO_3 (μmoles g^{-1})	Endogenous NO_2 (μmoles g^{-1})	Soluble protein (mg g^{-1})
Ammonium						
Shoot	0.03	41	2.9	0.07	180	21.00
Root	0.03	72	3.1	0.00	160	4.43
Ammonium + Aeration						
Shoot	0.05	43	1.9	0.00	170	25.00
Root	0.06	98	2.6	0.07	220	3.83
Nitrate						
Shoot	0.61	43	2.6	4.2	270	19.00
Root	2.11	21	2.4	34.8	190	3.35
Nitrate + Aeration						
Shoot	0.27	25	2.4	0.6	220	16.25
Root	1.14	27	3.0	7.0	170	2.57
Ammonium Nitrate						
Shoot	0.25	31	1.9	2.7	180	17.25
Root	0.09	47	2.9	5.1	180	3.85
Ammonium Nitrate + Aeration						
Shoot	0.18	51	2.8	0.3	270	23.75
Root	0.05	76	3.3	2.4	200	4.05

b. Experiment 2. Plants were germinated and transferred to cultures of either ammonium or nitrate (Table 1). Both treatments were nonaerated. The first 3-week growth occurred under growth chamber conditions as previously described; because of a growth chamber malfunction, plants were transferred to greenhouse conditions for the remaining 11 weeks. Nutrient solutions were changed every 2 weeks. At 10 weeks' growth, both ammonium and nitrate concentrations were increased to 8 millimoles (mM) for 1 week, and increased to the normal 4-mM concentration for the last 3 weeks. At the end of 15 weeks' growth, plants were harvested, rinsed in distilled water, dried at 70° Celsius, and weighed. Analyses for nitrogen (N), phosphorus (P), potassium (K), calcium (Ca), sodium (Na), magnesium (Mg), copper (Cu), iron (Fe), zinc (Zn), and manganese (Mn) were performed by the Analytical Service Laboratory, North Carolina State University, Soil Science Department (Table 13).

Table 13. Dry weight and nutrient concentration after 14 weeks' growth under nonaerated conditions.

Treatment	Dry wt g/plant	Nutrient Concentration									
		N	P	K	Na	Ca	Mg	Zn	Cu	Fe	Mn
		---------Conc., %-----------						---Conc., ppm----			
Ammonium											
Shoots	4.69	2.10	0.41	2.10	2.43	0.23	0.08	79	13	70	79
Roots	2.00	1.17	0.31	1.60	1.94	0.13	0.10	--	--	--	--
Nitrate											
Shoots	4.09	1.42	0.41	1.29	3.16	0.37	0.07	71	10	58	152
Roots	1.39	1.02	0.33	1.80	2.40	0.13	0.15	--	--	--	--

Nitrogen concentration of shoots and roots was highest for the ammonium treatment, indicating a greater uptake. Of particular interest are the differing sodium and potassium concentrations obtained with the different nitrogen sources. Potassium concentration was highest with the ammonium treatment; sodium was highest with the nitrate treatment. With other species, the presence of ammonium usually results in a lower potassium concentration. However, such studies are not commonly conducted with the low ambient potassium-sodium ratio (Table 1) used here. Calcium concentration in the shoots was greater with the nitrate treatment although no difference was observed for root tissue. In contrast, magnesium concentration of the shoots was not affected by the nitrogen source; root magnesium was significantly

increased by nitrate. Manganese concentration in the shoots was greater with the nitrate treatment. Phosphorus, zinc, copper, and iron concentrations were not significantly affected by nitrogen source. Significant changes in mineral composition result from the two sources but whether these were instrumental in the growth effects is presently unknown.

c. Experiment 3. After germination, plants were transferred to nonaerated ammonium solutions (Table 1) for a 6-week growth period. The plants were grown under growth chamber conditions. At the end of 6 weeks, the plants were transferred to a similar nutrient solution lacking nitrogen for 5 days.

A 21-hour uptake period with four treatments was initiated. The treatments were ammonium-nonaerated, ammonium-aerated, nitrate-nonaerated, and nitrate-aerated. Each treatment was replicated twice with three plants per replicate. Three plants were placed in 50- or 100-milliliter containers in which an initial 0.5-millimole ammonium or nitrate concentration was present. The solution concentration was then measured and renewed at different time intervals throughout the 21-hour uptake period. The nitrogen sources were labeled with 98-percent ^{15}N in all uptake solutions. Ammonium was provided as $^{15}NH_4Cl$ and nitrate as $K^{15}NO_3$; the only other nutrient present was 1×10^{-4} M $CaSO_4$. The uptake solutions were continuously stirred with magnetic stirring bars. Lights were maintained at 3,000-foot candles throughout the uptake period.

At the completion of the uptake period the plants were removed, rinsed in distilled water for 1 minute, and the shoots were separated from the roots. Analyses for carbohydrate, protein, GDH, NR, and endogenous NH_4 and NO_3 were determined on a part of the tissue. Another part was then separated into a soluble and an insoluble fraction using a methanol:chloroform:water (13:4:3) procedure, and the incorporation of ^{15}N into the soluble and insoluble fractions were determined.

Ammonium uptake exceeded nitrate uptake at the end of the experiment by a factor of 4 for nonaerated solutions and 5 for aerated solutions (Fig. 26). The rate of ammonium uptake was high initially and then decreased to a linear rate after 6 hours. This high initial rate was probably due to the 5-day minus-nitrogen pretreatment period which decreased plant nitrogen reserves. Nitrate uptake was very low for the first 6 hours (nondetectable in the first 2 hours) but the rate then slowly increased throughout the uptake period. The data suggest that nitrate uptake was substrate-inducible. Aeration slightly decreased uptake from ammonium and nitrate solutions but did not change the general uptake pattern.

Roots exposed to $K^{15}NO_3$ lost sodium to the ambient solution during the uptake period; the cumulative loss (Fig. 27) showed a high initial

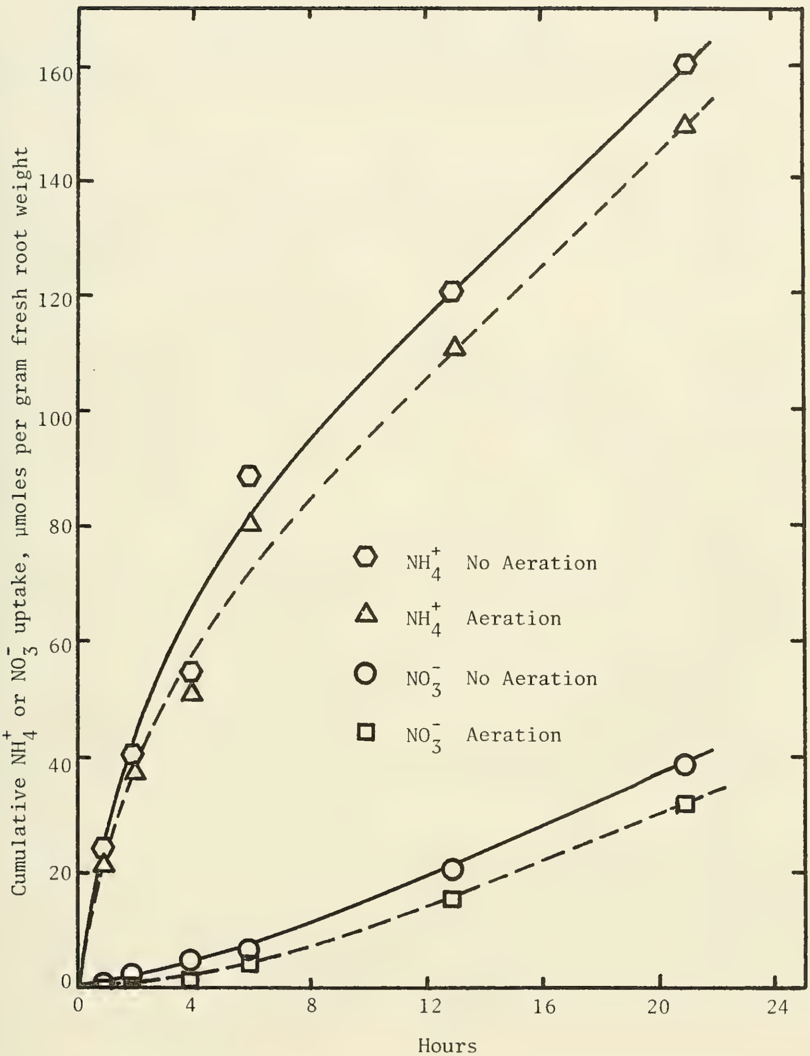


Figure 26. Experiment 3. Effect of aeration on ammonium uptake from 0.5-m$\underline{M}$ NH_4Cl and on nitrate uptake from 0.5-m$\underline{M}$ KNO_3.

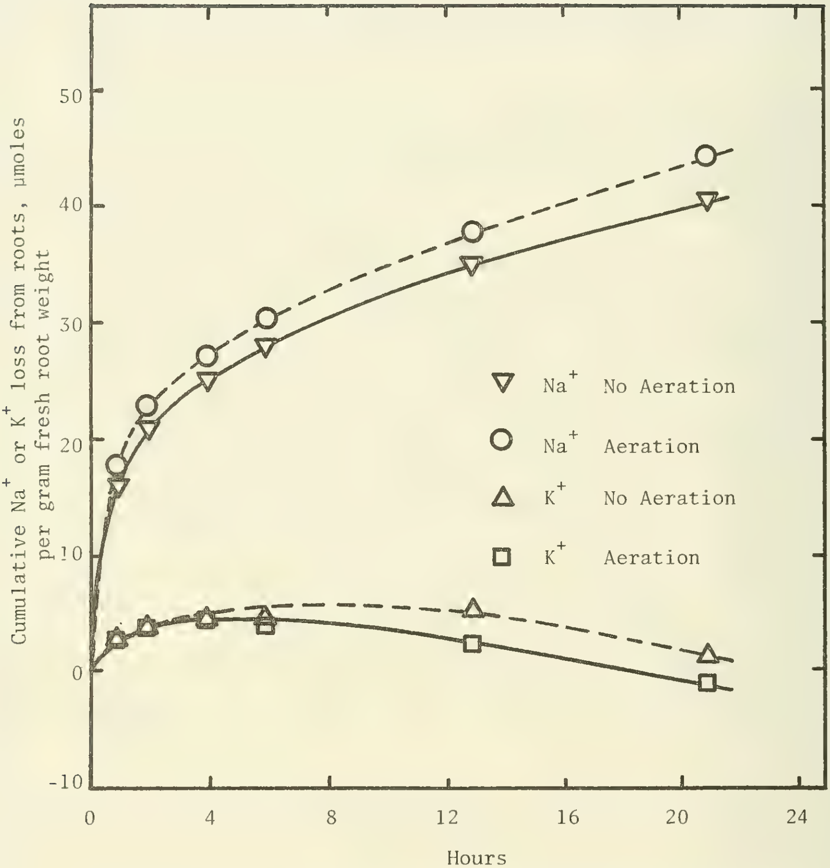


Figure 27. Experiment 3. Effect of aeration on net loss of sodium or potassium from roots during exposure to 0.5-m$\underline{M}$ KNO_3.

rate which decreased with time. Conceivably, sodium efflux may have been passive since the roots were exposed to KNO_3 solutions devoid of sodium during the uptake period. Furthermore, nitrate uptake was low particularly in the early phases and most likely did not influence sodium efflux. A slight potassium efflux occurred in the first 4 hours (Fig. 27); however, a net influx of potassium was apparent by the end of the uptake study.

During ammonium uptake from $N^{15}H_4Cl$ solutions, both sodium and potassium efflux were apparent (Fig. 28). Sodium efflux was greater than potassium efflux, and aeration decreased efflux of both ions. Electrical neutrality seems to have been maintained through hydrogen ion excretion (pH of external solution decreased) and by the efflux of both sodium and potassium.

Total nitrogen and ^{15}N in the tissue at the end of the 21-hour uptake period are shown in Table 14. Although all plants were pretreated in nonaerated ammonium solutions (unlabeled $^{14}NH_4$), some variability in the nitrogen status can be noted. The uptake of labeled ^{15}N comprised approximately 10 percent or less of the total nitrogen in the plants. Of this total nitrogen (^{14}N + ^{15}N), approximately 65 percent was in the shoots. Also, a higher proportion of the total nitrogen was present in the insoluble fraction in the shoots.

Of the total ^{15}N taken up by the plants, the greatest proportion was transported to the shoots (39 percent) when the nitrogen form in the uptake solution was ammonium (Table 14). Nonaerated nitrate treatments resulted in only 26 percent of the total ^{15}N being transported to the shoots. Aerated nitrate treatments resulted in even less transport to the shoots (10 percent). Thus, aeration seemed to affect translocation when the nitrogen uptake form was nitrate but did not affect it when the form was ammonium. The proportion of ^{15}N incorporated into the insoluble fraction was greatest in the shoots with ammonium treatments but there was little difference between shoots and roots with nitrate treatments. Aeration appeared to decrease ^{15}N incorporation into the soluble fraction of the shoots with the nitrate treatment.

The rapid uptake of ammonium substantially enhanced root GDH under nonaerated conditions but, with aeration, activity was depressed (Table 15). The depression occurred in spite of a higher ammonium accumulation in the roots of the aerated treatment. There was a slight increase in root GDH activity of both nitrate treatments but shoot GDH was not affected by any of the four treatments. Protein content was not changed, probably because the uptake period (21 hours) was not long enough for a significant effect to be noted. Soluble carbohydrate content was unaffected.

Nitrate reductase activity was essentially nil at the start of the experiment and in those tissues exposed to ammonium uptake solutions

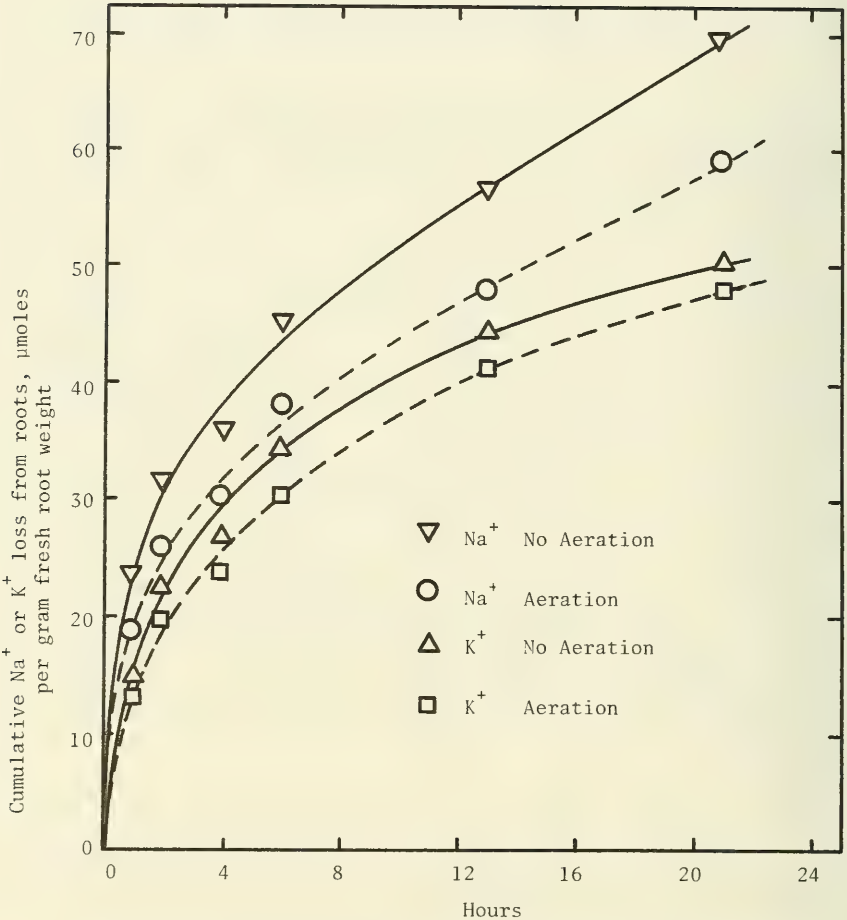


Figure 28. Experiment 3. Effect of aeration on net loss of sodium or potassium from roots during exposure to 0.5-m$\underline{M}$ NH_4Cl.

Table 14. Experiment 3. Total nitrogen and ^{15}N incorporation into soluble and insoluble fractions after 21 hours' exposure to 0.5-mM $^{15}NH_4Cl$ or $K^{15}NO_3$ (98 atom % ^{15}N).

Treatment	$^{14}N + ^{15}N$ Insoluble	$^{14}N + ^{15}N$ Soluble	$^{14}N + ^{15}N$ Total	$^{14}N + ^{15}N$ Percent of Total N in Insoluble	^{15}N Insoluble	^{15}N Soluble	^{15}N Total	^{15}N Percent of Total N in Insoluble
	(ug/g dry wt.)			---(%)	(ug/g dry wt.)			---(%)
Ammonium - No Aeration								
Shoots	3415.0	890.0	4305.0	79.3	137.0	161.0	298.0	46.0
Roots	1510.0	730.0	2240.0	67.4	174.0	278.0	452.0	38.5
Total	4925.0	1620.0	6545.0	75.2	311.0	439.0	750.0	41.5
% of total in shoots	69.3	54.9	65.8		44.0	36.7	39.7	
Ammonium - Aerated								
Shoots	4015.0	900.0	4915.0	81.7	178.0	161.0	339.0	52.5
Roots	1510.0	840.0	2350.0	64.2	180.0	344.0	524.0	34.4
Total	5525.0	1740.0	7265.0	76.0	358.0	505.0	863.0	41.5
% of total in shoots	72.7	67.2	67.7		49.7	31.9	39.3	
Nitrate - No Aeration								
Shoots	3235.0	900.0	4135.0	78.2	32.0	28.0	60.0	45.7
Roots	1260.0	550.0	1810.0	69.6	74.0	96.0	170.0	43.5
Shoots	4495.0	1450.0	5945.0	75.6	106.0	124.0	230.0	44.2
% of total in shoots	71.9	62.1	69.6		30.2	22.6	29.2	
Nitrate - Aerated								
Shoots	1770.0	780.0	2550.0	69.4	7.0	14.0	21.0	33.3
Roots	1030.0	615.0	1645.0	62.6	60.0	114.0	174.0	34.5
Total	2800.0	1395.0	4195.0	66.7	67.0	128.0	195.0	34.3
% of total in shoots	63.2	55.9	60.8		10.4	10.9	10.7	

(Table 15). Nitrate reductase activity was induced by exposure to nitrate, and it was higher in the roots than in shoots. Aeration depressed nitrate reductase by approximately 40 percent in root tissue suggesting a greater aeration effect on nitrate metabolism than on the uptake process itself (Fig. 26). However, endogenous root nitrate seemed slightly enhanced by aeration. If aeration were affecting nitrate reduction rather than uptake, a buildup of endogenous nitrate would be expected.

d. Experiment 4. Plants were germinated and grown in a nonaerated ammonium culture (Table 1) for 6 weeks (described for experiment 1) in a greenhouse environment (September and October 1973) instead of growth chamber conditions. At the end of 6 weeks' growth, plants were transferred to minus nitrogen solutions for 2 days in preparation for a 24-hour uptake period. The same treatments, except with four replications were used as in experiment 3. Nitrogen was labeled with 98-percent ^{15}N; the initial concentration of ammonium and nitrate was 1 mM. Four plants were placed in 880-milliliter containers and allowed to deplete the concentration without renewal. The solutions were not depleted of nitrate or ammonium by the end of the experiment. In contrast to experiment 3, all other nutrients were provided as given in Table 1 and the uptake period occurred under greenhouse conditions. The experiment was initiated at 0900 hours and had a 10-hour dark period from 2200 hours until 0600 hours the following morning. After harvesting, tissue was separated into an insoluble and soluble fraction.

The results of this experiment (Fig. 29) agree with the results of experiment 3 in showing a low initial nitrate uptake which slowly increased. The ammonium uptake rate again slowed substantially after about 6 hours. Aeration suppressed the uptake of both NH_4 and NO_3, the effect being somewhat greater than in experiment 3. Uptake of both ions (based on root weight) was greater than in experiment 3, perhaps due to their greater initial weight (approximately threefold). Differences in environmental conditions during the experiment and the presence of other ions in the uptake media could have contributed to these differences between the two experiments. The data are consistent overall in showing that aeration restricted the uptake of both forms of nitrogen, and that *Spartina alterniflora* can develop the capacity to absorb nitrate. However, ammonium continued to be absorbed more effectively than nitrate during the course of these two experiments.

e. Experiment 5. One hypothesis relating to the relative growth rates of ammonium versus nitrate-cultured plants is that newly germinated plants cannot utilize nitrate effectively and are primarily dependent on an ammonium source to promote growth. At later stages of growth (5 to 6 weeks), plants may begin to develop the necessary metabolic machinery to utilize nitrate. Experiment 5 was designed to test this hypothesis.

Table 15. Experiment 3. Composition of ammonium-grown plants 5 days after transfer to a nitrogen-free solution and after a subsequent 21-hour exposure to 0.5-m*M* NH_4Cl or KNO_3.

Treatment		Soluble Carbohydrate (mg/g)	Soluble Protein (mg/g)	Nitrate Reductase (µmoles/g/hr)	Glutamic Dehydrogenase (µmoles/g/hr)	Ammonium (µmoles/g)	Nitrate (µmoles/g)
Exposed to nitrogen-free solution for 5 Days							
	Shoot	23.70	9.38	0.07	26.8	1.89	0.40
	Root	4.25	2.70	0.02	25.4	2.04	0.50
Exposed to ammonium for 21 hours							
No Aeration	Shoot	14.70	10.50	0.01	25.4	1.43	0.25
	Root	6.83	2.20	0.01	95.2	7.32	0.38
Aeration	Shoot	19.30	11.50	0.03	21.8	1.15	0.10
	Root	8.25	2.75	0.00	10.3	12.50	0.32
Exposed to nitrate for 21 hours							
No Aeration	Shoot	15.20	10.00	0.21	23.2	1.07	1.12
	Root	5.50	2.68	0.63	31.2	2.25	4.86
Aeration	Shoot	17.80	9.25	0.19	24.0	1.80	1.38
	Root	5.50	2.40	0.37	31.9	2.35	5.38

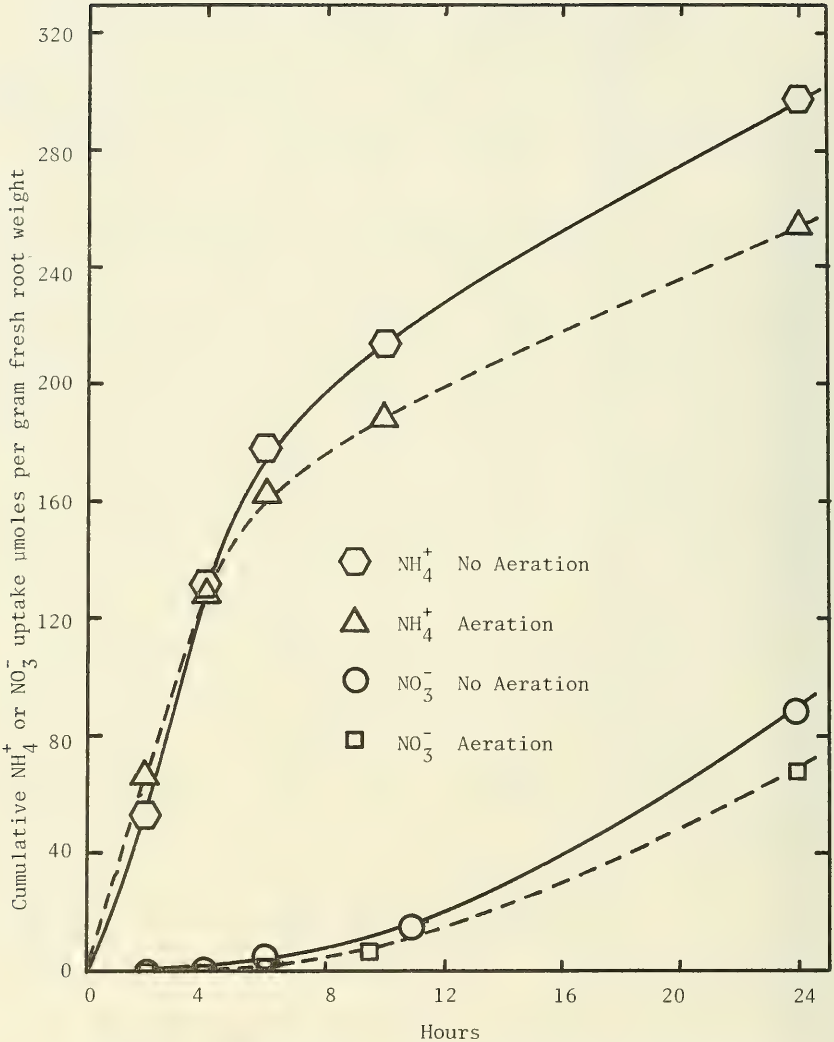


Figure 29. Experiment 4. Effect of aeration on ammonium uptake from 0.5-m$\underline{M}$ NH_4Cl and on nitrate uptake from 0.5-m$\underline{M}$ KNO_3.

Plants were germinated and grown for 6 weeks under conditions described for experiment 4. A series of plants was selected for a 17-day uptake period utilizing the treatments described for experiment 4. Plants were not deprived of nitrogen before the uptake period but were transferred directly from the ammonium pretreatment (Table 1) solutions to the labeled treatment solutions. At this stage, the shoots and roots averaged 3.21 and 1.04 grams fresh weight per plant and all plants were green and healthy. The uptake solutions contained either 4-mM ammonium or 4-mM nitrate labeled with 98-percent ^{15}N and contained all other nutrients as given in Table 1. Aeration and nonaeration treatments were used. Four plants were placed in a pot containing 880 milliliters of the appropriate uptake solution. The ammonium or nitrate concentration in the uptake solution was then monitored at various time intervals (correcting for water loss) throughout the 17-day period.

At the end of the 17 days, plants were harvested and separated into insoluble and soluble fractions for ^{15}N analyses. Although the data from this experiment have not been completely analyzed yet some significant observations are available. The gain in fresh weight in 17 days was significantly greater with ammonium treatments as compared to nitrate treatments (Table 16). No significant differences in total weight were noted for aeration versus nonaeration with either nitrogen source. However, aeration did affect the relative distribution of fresh weight gain between shoots and roots. With aeration, greater root weight relative to shoot weight resulted as compared to nonaeration (Table 16). No noticeable effects were observed with respect to leaf yellowing as was observed with nitrate cultures or aeration in young seedlings. Thus, the ammonium culture promoted greater fresh weight production than the nitrate even after the 6-week growth stage; it did so even when the nitrate treatment did not induce the severe chlorotic symptoms observed when nitrate was supplied early in growth.

Table 16. Experiment 5. Growth of shoots and roots in 17 days as influenced by nitrogen source and aeration. Plants were grown for 6 weeks with ammonium and without aeration, at which time shoot and root fresh weight averaged 3.21 and 1.04 grams per plant.

Treatment (17 days)	Final Weight (Grams Per Plant)		Increase in 17 Days (Grams Per Plant)		
	Shoots	Roots	Shoots	Roots	Total
Ammonium	5.65	1.86	2.43	0.82	3.25
Ammonium + Aeration	5.07	2.62	1.86	1.58	3.44
Nitrate	4.60	1.69	1.19	0.65	1.84
Nitrate + Aeration	4.26	2.12	1.05	1.08	2.13

Figures 30 and 31 present the cumulative ammonium and nitrate uptake during the 11th and 17th day after transfer. The ambient concentrations were allowed to sink to relatively low levels by the 11th day and were then replenished. Substantial nitrate uptake occurred, and both ammonium and nitrate uptake were restricted (29 percent and 33 percent, respectively) by aeration. Hence, failure of the nitrate-treated plants to grow as well as those treated with ammonium under these conditions was not a result of an inability to absorb nitrate.

f. Discussion. Forced aeration of the root system was clearly detrimental to plant growth under the conditions used in these experiments. During early growth the effects of aeration were more severe, especially when nitrate was the sole nitrogen source, than when aeration was imposed after the plants had developed vigorously under nonaerated conditions. Even in the latter case where growth rates were not restricted by aeration, there was a differential effect on root and shoot growth, with aeration promoting the former at the apparent expense of the latter. Both ammonium and nitrate uptake were slightly restricted by forced aeration during short-term experiments (Figs. 26 and 29). With nitrate, there was a marked restriction in nitrate reductase activity (Tables 11 and 14) and probably in translocation of the nitrogen absorbed as nitrate (Table 13). Soluble protein was restricted by aeration after 6 weeks' growth with ammonium as well as with nitrate (Table 11) suggesting an impact on nitrogen assimilation for both. However, aside from the effect on ammonium uptake, the present ^{15}N data (Table 13) do not indicate how this effect might come about.

Nitrate nitrogen was not a suitable sole source of nitrogen even under nonaerated conditions. Total nitrogen concentrations and soluble protein (Table 11) were generally lower in nitrate-treated plants (Table 12). Nitrate reductase activity and nitrate uptake (Figs. 26 and 29) could be induced by exposure to nitrate (Table 14). Presence of ammonium in the ambient medium severely lowered nitrate reductase, especially in the root tissue (Table 11). The extent resulting from depressed nitrate uptake is unknown. Low nitrate accumulation and low nitrate reductase in the shoots (Table 11) imply an inability to translocate nitrate, which is in agreement with the low total ^{15}N translocation (Table 13).

Tentatively, it is concluded that the inability to utilize nitrate effectively is partially a result of a low uptake capability. However, the plants do have the ability to generate nitrate uptake capacity (Fig. 31) and still not grow as effectively as with ammonium (Table 15). A further ineffectiveness in their nitrate assimilation pathway seems indicated.

2. Field Studies.

This aspect of marsh establishment and development is of interest for several reasons. One is that adequate nutrient supply is

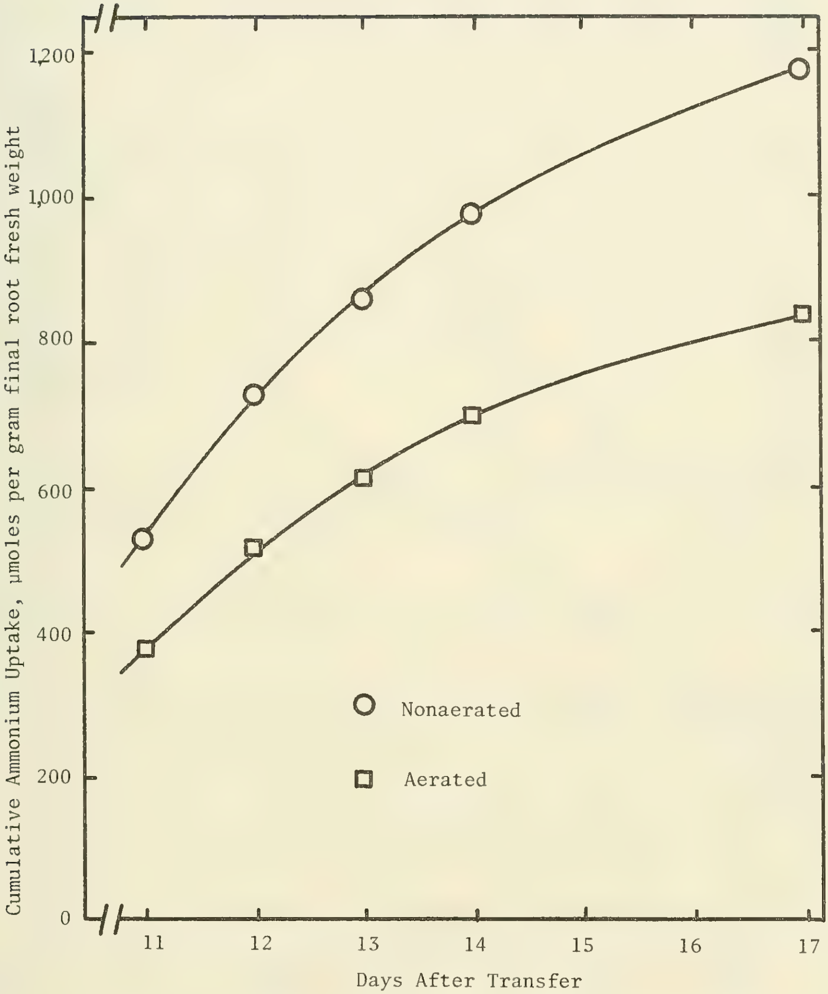


Figure 30. Experiment 5. Effect of aeration on ammonium uptake from ammonium-containing complete solutions during the 11- to 17-day period after transfer.

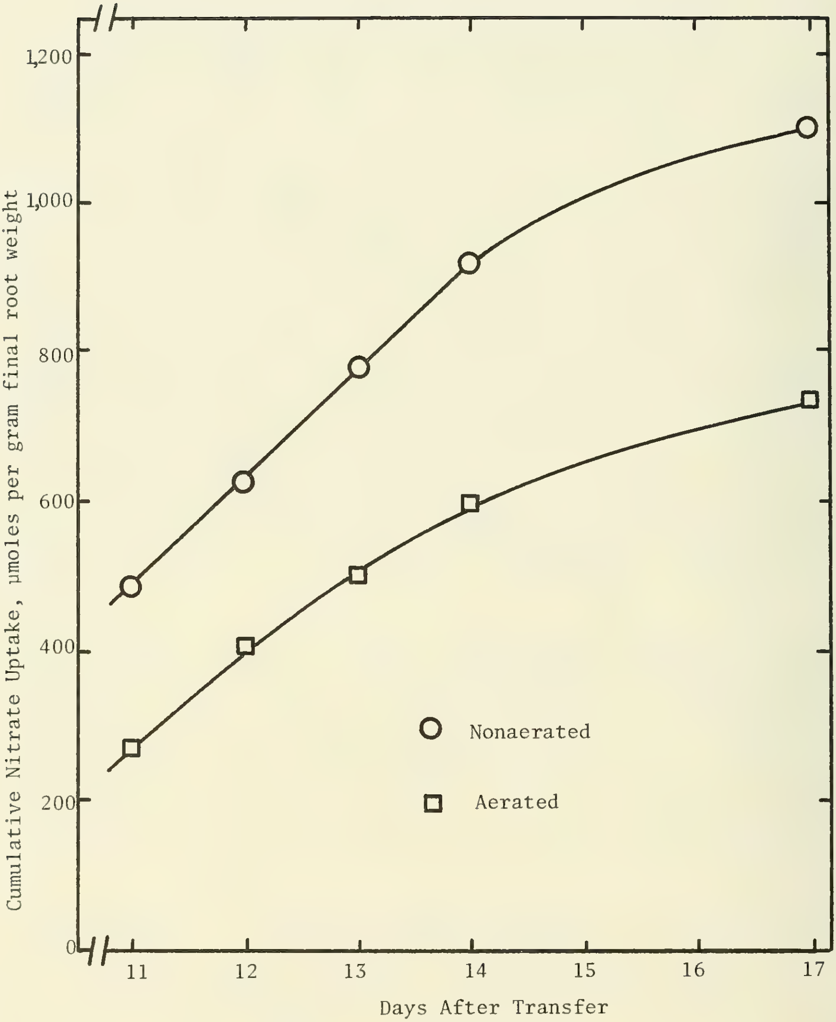


Figure 31. Experiment 5. Effect of aeration on nitrate uptake from nitrate-containing complete solutions during the 11- to 17-day period after transfer.

essential in the establishment and early development of marsh plantings. Another and perhaps more important reason is the role that marshes and marsh plants play in the storing and recycling of nutrients, and in serving as nutrient sinks to reduce the polluting effect of excess nutrient supplies in estuaries. Data relating to some of these functions were discussed by Woodhouse, Seneca, and Broome (1974). The data in this section are largely supplemental to the coverage in the earlier report.

a. Effect of 4 Years of Fertilization on a Young Natural Stand of *Spartina alterniflora* at Ocracoke, North Carolina. This experiment was established in 1971 on a young natural stand of *Spartina alterniflora* growing on a sandy substrate near Hatteras Inlet. The regular lunar tidal range is about 30 centimeters at this site but may be increased to 1 meter or more by wind setup. A factorial design was used with two rates of phosphorus and four rates of nitrogen. Phosphorus was applied as concentrated superphosphate and nitrogen as ammonium sulfate. The fertilizer was broadcast on the soil surface during low water. The applications were split, one-third late April or early May, one-third June, and one-third late July or early August. Aerial growth was harvested with a sickle-bar mower in September of each year.

Total growth and response to nitrogen increased in the fourth year, over the previous year, in the presence of applied phosphorus (Table 17). In the absence of applied phosphorus, nitrogen had a slight depressing effect. Both nitrogen and phosphorus were sharply limiting factors at this stage.

This fourth-year response is of interest in demonstrating the capacity of this vegetation to withstand and benefit from a rather high input of nutrients on a continuing basis.

b. Effect of 3 Years of Fertilization on the Short and Tall Forms of *Spartina alterniflora*. The fertilizer treatments and the design of this experiment, begun on Oak Island in 1972, are the same as in the 1971 Ocracoke experiment. The Oak Island marsh differs from the Ocracoke marsh in several ways. The tidal range is greater, the substrate is finer textured, the marsh is much older, and the drainage pattern is better developed. The tall form of *Spartina alterniflora* occupies the tidal creek banks; the plots at Oak Island include both the short and tall form.

Growth of the short form of *Spartina alterniflora* was increased by the application of nitrogen without the addition of phosphorus. There was a further significant increase at the higher rates of nitrogen when phosphorus was applied (Table 18). The finer sediments of the Oak Island marsh supply more phosphorus than the sandy Ocracoke substrate.

Growth of the tall form of *Spartina alterniflora* was increased significantly by phosphorus application in this experiment in 1974

Table 17. Effect of the fourth year of fertilizer[1] on growth of *Spartina alterniflora* at Ocracoke. Plots 4 by 25 feet, three replications. (Harvested 19 September 1974)

N rate (kg/ha)		Aerial dry wt (kg/ha) P rate (kg/ha)		
		0	74	Average
0		4,085	3,831	3,958
168		4,671	8,592	6,632
336		3,635	11,192	7,413
672		3,484	17,029	10,257
Average		3,969	10,161	
LSD[2]				
Nitrogen	0.01	1,573		
	0.05	1,133		
Phosphorus	0.01	1,112		
	0.04	801		
Nitrogen X Phorphorus	0.01	2,224		
	0.05	1,603		
CV[3]	(%)	13.0		

1. Nitrogen from ammonium sulfate and phosphorus from treble superphosphate applied in split applications in April, June, and August of each year.

2. Least significant difference.

3. Coefficient of variation.

Table 18. Third-year effect of nitrogen and phosphorus fertilizers[1] on the short form of *Spartina alterniflora* at Oak Island (30 Sept 1974). Plots 4 by 50 feet, three replications.

N rate (kg/ha)		P rate (kg/ha)					
		Aerial dry weight (kg/ha)		Flowers/m^2		No. culms/m^2	
		0	74	0	74	0	74
0		4,453	4,240	16	13	527	445
168		10,080	10,813	56	41	557	476
336		10,813	14,667	24	53	512	401
672		13,973	21,667	47	43	447	445
Average		9,830	12,847	36	38	511	442
LSD:[2]	N 0.01		4,786	*[3]			*[3]
	0.05		3,448	24			*[3]
	P 0.01		*[3]	*[3]			*[3]
	0.05		2,438	ns			ns
CV[4]	(%)		24.6	52.7			20.9
		Height (cm)		Basal area (cm^2/m^2)		Salinity (ppt)	
		0	74	0	74	0	74
0		58	57	96	141	26	26
168		102	109	223	241	26	26
336		97	125	252	230	25	25
672		129	135	274	314	25	25
Average		97	107	211	231	26	26
LSD:[2]	N 0.01		30		83		*[3]
	0.05		21		60		*[3]
	P 0.01		*[3]		*[3]		*[3]
	0.05		*[3]		*[3]		*[3]
CV[4]	(%)		17.0		21.9		4.0

1. Fertilizer applied 13 May, 19 June, and 19 August 1974.

2. Least significant difference.

3. Not significant.

4. Coefficient of variation.

(Table 19). This is the first fertilizer response for the tall form in any of the North Carolina experiments. Salinity was consistently lower under the tall form than under the short form but remained well below sea strength under both.

c. Effect of 2 Years of Fertilization on a Seeded Stand of *Spartina alterniflora*. This seeding was done in April 1973 on an island in Core Sound near new Drum Inlet, North Carolina (Woodhouse, Seneca, and Broome, 1974). The island surface lies within the intertidal zone and is inundated by seawater at each high tide, except for periods of strong southwesterly winds which lower the water level. During low water and the absence of precipitation, the increased salt concentration near the soil surface becomes highly detrimental to the development of *Spartina alterniflora*, killing some plants each summer.

This experiment, which began 11 July 1973, included two rates of phosphorus and four rates of nitrogen in a complete factorial design. There were strong indications that year that the addition of nutrients improved the ability of the seedlings to overcome salt stress (Woodhouse, Seneca, and Broome, 1974). Fertilizer was applied in split applications again in 1974 (30 April, 5 June, and 31 July). Response was greater than in 1973 with a sevenfold increase for nitrogen plus phosphorus. Nitrogen response continued upward, in the presence of applied phosphorus, through the highest nitrogen rate, 672 kg/ha N (Table 20).

The application of nutrients does not have any direct effect upon the salt buildup problem. It did enable the plants to grow at a more rapid rate when conditions were favorable. The addition of nutrients brought about rapid stabilization in doubtful areas.

VI. MARSH DEVELOPMENT

The early stages of the development into marsh of several planted areas were described in Woodhouse, Seneca, and Broome (1974). This section adds a year to that initial account on three sites. The first site is the plant source experiment at Snow's Cut, planted in 1971 (Table 6). Dry matter production in the fourth year seems to be leveling off at about 12 metric tons per hectare. Visually, the planted area is indistinguishable from nearby natural marsh; it appears to be approaching a fairly stable condition.

The second site was seeded near Beaufort in 1972. Plant growth at this site was low in 1974 (Table 8), only a little over 4 metric tons per hectare, no more than in 1973. Development of this seeded marsh ceased at a low level of production, less than one-third that of the Snow's Cut planting. This may reflect the origin of this planting, Oregon Inlet seed. Although Oregon Inlet plants have grown satisfactorily at Snow's Cut, a low salinity-high nutrient site experience at Pine Knoll Shores in 1974 has indicated that plants from the Oregon

Table 19. Third-year effect of nitrogen and phosphorus fertilizers[1] on the tall form of *Spartina alterniflora* at Oak Island (30 Sept 1974). Plots 4 by 25 feet, three replications.

N rate (kg/ha)	P rate (kg/ha)					
	Aerial dry weight (kg/ha)		Flowers/m²		No. culms/m²	
	0	74	0	74	0	74
0	18,667	23,680	28	39	251	243
168	25,587	23,427	39	36	323	281
336	15,947	27,720	20	44	197	277
672	21,107	26,133	27	36	233	263
LSD:[2] N 0.01		*[3]		*[3]		*[3]
0.05		*[3]		*[3]		*[3]
P 0.01		4,002		6		*[3]
0.05		2,884		4		*[3]
N x P 0.01		*[3]		12		*[3]
0.05		5,767		9		*[3]
CV[4] (%)		14.5		14.5		22.5

	Height (cm)		Basal area (cm²/m²)		Salinity (ppt)	
	0	74	0	74	0	74
0	158	180	226	274	22	21
168	178	176	328	324	21	23
336	165	187	208	324	21	22
672	176	177	328	299	21	22
LSD:[2] N 0.01		*[3]		*[3]		*[3]
0.05		*[3]		*[3]		*[3]
P 0.01		*[3]		*[3]		*[3]
0.05		*[3]		*[3]		*[3]
N x P 0.01		*[3]		*[3]		*[3]
0.05		*[3]		*[3]		*[3]
CV[4] (%)		7.5		18.0		7.7

1. Fertilizer applied 13 May, 19 June, and 19 August 1974.

2. Least significant difference.

3. Not significant.

4. Coefficient of variation.

Table 20. Effect of nitrogen and phosphorus fertilizers[1] in second-year growth on seeded *Spartina alterniflora* at South Island (Drum Inlet). Plot size 4 by 25 feet, three replications. (Seeded 18 Apr 1973, sampled 25 Sept 1974).

N Rate (kg/ha/yr)	P Rate (kg/ha)									
	0	74	0	74	0	74	0	74	0	74
	Aerial Dry weight (kg/ha)		Flowers/ m^2		No. culms/ m^2		Height		Basal area (cm^2/m^2)	
0	1,367	2,030	139	215	304	410	53	65	42	58
168	2,940	5,170	208	414	393	760	66	83	76	130
336	2,503	6,717	160	419	321	811	69	89	56	180
672	3,323	10,333	212	376	450	814	74	88	97	237
LSD[2]										
N 0.01	2,065		*[3]		*[3]		*[3]		65	
0.05	1,488		*[3]		182		15		47	
P 0.01	1,460		104		179		15		46	
0.05	1,052		75		129		11		33	
N x P										
0.01	2,920		*[3]		*[3]		*[3]		*[3]	
0.05	2,104		*[3]		*[3]		*[3]		66	
CV%[4]	28.0		31.9		27.6		16.4		34.4	

1. Fertilizer applied 30 April, 5 June, and 31 July 1974.

2. Least significant difference.

3. Not significant.

4. Coefficient of variation.

Inlet seed source, even though grown at Beaufort, were not as well adapted to the general locality the first season. The Beaufort and Pine Knoll sites are subject to sea strength salinity which may make a difference.

The third site is on South Island (Drum Inlet). Growth of these plants improved substantially in 1974 when sufficient nutrients were applied (Table 20). Aerial dry weight under the heaviest fertilization increased fourfold between 1973 and 1974, but there was essentially no change on the unfertilized control. A supplementary supply of nutrients seems to be essential to the development of a marsh on this difficult site. Repeated fertilization for this purpose would be impractical in some instances. It could be the most economical route to stabilization in others.

VII. PLANTING SPECIFICATIONS FOR *SPARTINA ALTERNIFLORA*

The following guidelines are based on this work, experience along the North Carolina coast, and limited observations at various points along the Atlantic and gulf coasts.

1. Transplanting.

a. Plants. Healthy, single stems from uncrowded stands should be used, keeping as much of the root system intact as possible. Rhizomes, small shoots, and flowering stalks from the previous year may be removed or trimmed to not interfere with transplanting. Plants from the immediate area are preferable to planting stock from other locations. Trial plantings should be made where adaptation of planting stock is unknown. Plants may be stored several weeks by heeling-in in the intertidal zone. Plants can be produced under the more expensive greenhouse conditions.

b. Planting. In hand planting or machine planting 10 to 15 centimeters (4 to 6 inches) deep, the soil is immediately firmed around the plant to prevent the plant from floating out of the hole or furrow.

c. Spacing. Under fairly protected conditions, plants set on 1-meter centers will provide complete cover early in the second growing season. Closer spacings, 24 inches to as close as 18 inches (0.6 to 0.45 meter) are warranted only on critical sites since planting costs are almost directly proportional to the number of plants planted.

Spacing		Plants per 1,000 square feet
Inches	Meters	
12	0.30	1,000
18	0.45	445
24	0.60	250
36	0.90	111

d. Planting Dates. March, April, and early May are ideal planting months for North Carolina. *Spartina alterniflora* can be transplanted year round, but not with equal success. Winter transplants are subject to severe weather, strong wave action, and erosion or deposition hazards. Summer planting reduces the time for establishment before winter. Circumstances will often warrant consideration of planting times which are less than optimum.

e. Elevation. *Spartina alterniflora* will usually grow between MHW and MLW for locations with low tidal ranges, and from MHW to MSL for higher tidal ranges. Since there will be variations in adaptation where wind setups are large, upper and lower limits of growth of natural stands of *Spartina alterniflora* in the vicinity should be checked.

f. Fertilization. Plantings often respond to the addition of nutrients in nutrient-poor situations, characterized by a sandy substrate, little or no clay or silt moving into the area, and a low concentration of nitrogen and phosphorus in the surrounding water. Nitrogen and phosphorus are the likely limiting nutrients. Chemical assays are useful only to identify extremes. Conventional tests for available phosphorus were developed for uplands and are not reliable for coastal conditions. There are no convenient chemical testing methods that will satisfactorily forecast available nitrogen supplies.

2. Seeding.

a. Seeds. Seeds should be harvested near maturity (late September and early October in North Carolina) and stored in estuarine water at 2° to 3° Celsius.

b. Method. Broadcast the seed at low tide and cover 1 to 3 centimeters by tillage. Till before and after broadcasting.

c. Rate. Seeding rate should be based on viable seeds since quality varies widely. Optimum rate is about 100 viable seeds per square meter. Adequate stands are possible under favorable conditions with one-half this rate.

d. Planting Date. The best time is probably immediately after natural seedlings appear (March along the North Carolina coast). Earlier seeding is susceptible to weather risks. *Spartina alterniflora* can be seeded as late as the end of June in North Carolina. This produces greatly reduced first-year growth. If the stand survives the winter, growth equals that of earlier seedings by the end of the second growing season.

e. Elevation. Seeding should usually be confined to about the upper half of the tidal range.

f. Fertilization. Seedlings are usually more responsive to fertilizer than transplants. First-year growth can be increased substantially by fertilization in nutrient-poor environments. Top dressings of about 100 kilograms per hectare of nitrogen (90 pounds per acre) and 25 kilograms per hectare of phosphorus (50 pounds per acre P_2O_5), applied in late June and again in late July, are suggested where nutrient deficiencies are suspected. Nitrogen should be from ammonium sulfate and phosphorus from a soluble source such as treble superphosphate. Application should be on the exposed soil surface at low tide.

VIII. SUMMARY AND CONCLUSIONS

The results from new experiments established on eroding shorelines on Bogue Sound indicated that rhizomes of *Spartina alterniflora*, without attached well-developed culms, were worthless as propagules within the intertidal zone. Neither fertilization in the nursery nor in the furrow at transplanting affected final establishment of vegetation on this shoreline. Plant growth from seeds in peat pots were the same as field-grown transplants, but were more expensive to produce and more difficult to transplant. Plants from a local source were superior the first growing season to plants grown locally from foreign seeds. Differences between sources of plant material transplanted at Snow's Cut largely disappeared in the fourth year after transplanting.

Seeding was unsuccessful on a Bogue Sound shoreline because of the exposed location. Transplants spaced 1.5 and 2 feet produced substantially better stands than the normal 3-foot spacing in the first year. *Spartina alterniflora* marsh, destroyed by land development activities 2 years earlier, was successfully reestablished through transplanting on an eroding shoreline in one growing season.

The dominance of the ammonium form of nitrogen and the low ambient oxygen concentration normal to soils in the intertidal zone were optimal for the growth of *Spartina alterniflora*. The inability of this plant to utilize nitrate effectively appears to be partially a result of a low uptake capability and an inability to translocate nitrate.

A young stand of *Spartina alterniflora* on a sandy substrate continued to withstand and respond to high inputs of nutrients through the fourth year. Similar results were obtained through the third year on an old stand of the short form growing on a fine-textured substrate. Fertilizer applications were highly beneficial in enabling the development of a seeded *Spartina alterniflora* stand, subjected periodically to severe salt stress.

Specifications for transplanting and for seeding *Spartina alterniflora* are included in this report.

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